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Environmental Impact Research Program

Test and Modification of a Northern Bobwhite Habitat Suitability Index Model

by L. Jean O'Neil
Environmental Laboratory

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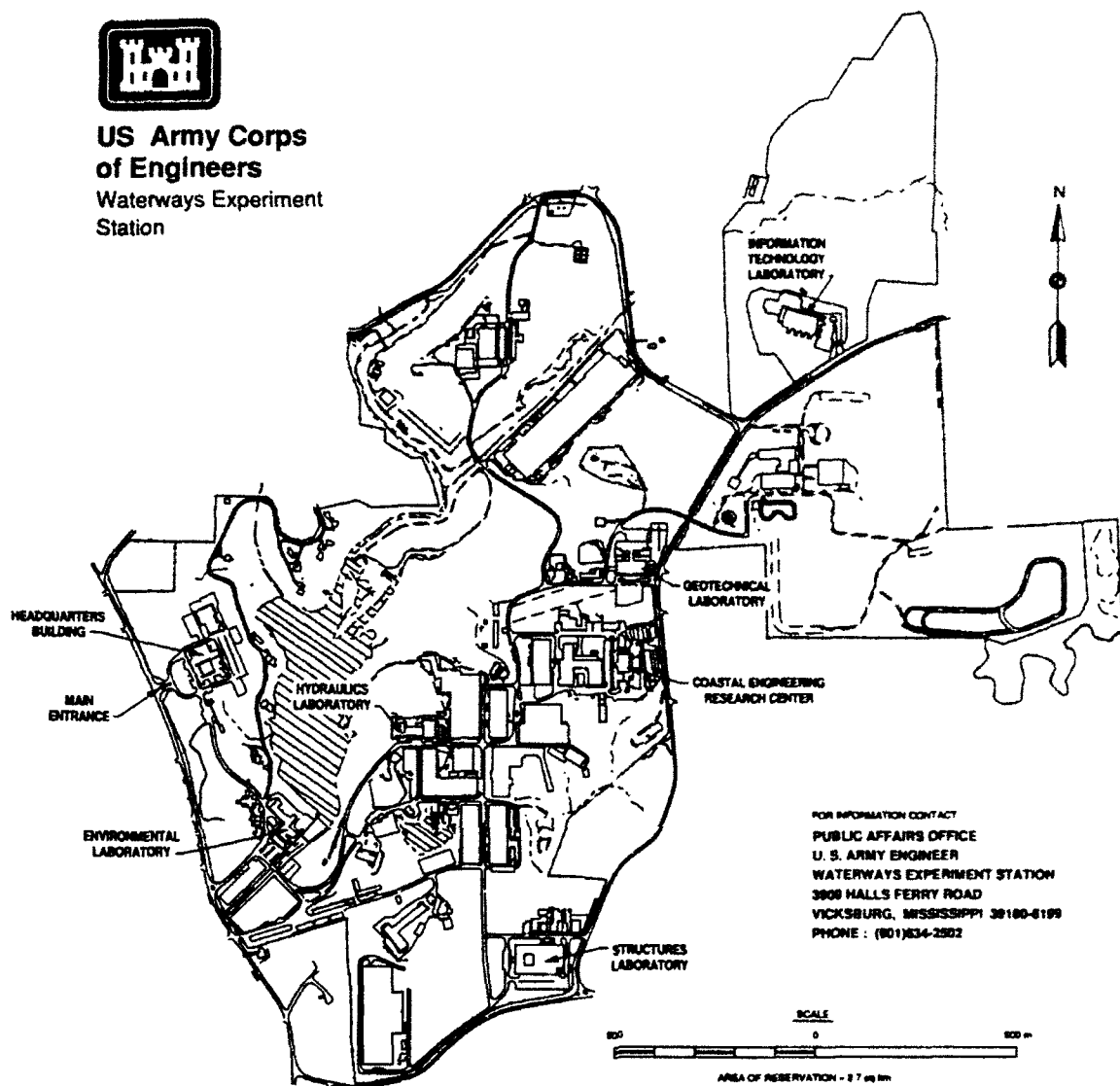3909 Halls Ferry Road
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Final report

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SCALE

AREA OF RESERVATION = 2.7 sq km

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Preface

The research for this dissertation was accomplished under Work
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The dissertation was prepared by Dr. L. Jean O'Neil, in partial fulfill-
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(Chair), R. Douglas Slack, Fred E. Smeins, and William E. Grant.

During preparation of this report, Dr. O'Neil worked under the supervi-
sion of Mr. Roger Hamilton, Chief, Resource Analysis Branch; Dr. C. J.
Kirby, Chief, Environmental Resources Division; and Dr. John Harrison,
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rector of WES. COL Leonard G. Hassell, EN, was Commander.

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TEST AND MODIFICATION OF A NORTHERN BOBWHITE
HABITAT SUITABILITY INDEX MODEL

INTRODUCTION

The National Environmental Policy Act of 1969 requires Federal agencies to consider previously unquantified environmental features along with traditionally quantified economic and technical considerations in planning activities that affect the environment. Within the U.S. Army Corps of Engineers (CE) and the U.S. Fish and Wildlife Service (FWS), the currency for wildlife has generally become Habitat Units (HU).

A HU is a numerical description of habitat quantity and quality, derived by multiplying area of habitat by a Habitat Suitability Index (HSI). This concept comes from the Habitat Evaluation Procedures (U.S. Fish and Wildlife Service 1980) or HEP. Development of models to determine a HSI began in the late 1970's to provide users of HEP with a means of numerically rating habitat quality for individual species. Consistency and reliability of these ratings have been shown to increase with a structured format, i.e., a model (Ellis et al. 1979, Mule' 1982), and the number of published models has steadily increased to over 150. As a consequence, HSI models are often applied in planning, impact assessment, and management.

Models can be developed using information on habitat requirements from the literature, field and laboratory studies, a committee of experts on the species, or a combination of approaches. Ideally, model construction is an iterative process of development, testing,

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This dissertation follows the style of the Journal of Wildlife Management.

modifying, and retesting, until the final product meets the model builder's objectives. Most models in the HSI series have been constructed at a fairly rapid pace and for relatively large geographic regions in order to provide a wider selection of models to hasten implementation of HEP. As a result, HSI models are often applied without adequate testing and carefully thought out modification to match the model to its task.

A project on habitat evaluation at the CE Waterways Experiment Station (WES) includes testing and modifying models. One of the species selected is the northern bobwhite (*Colinus virginianus*). Because models are a simplification of reality (Hall and Day 1977), some measurement of reality is necessary to compare with the model output and to determine the amount of agreement between the model and its subject. The standard of comparison used to test this model was census data.

The null hypothesis was that no relationship existed between bobwhite population density and HSI model scores. The alternate hypothesis was that a significant and positive relationship existed. Furthermore, if the null hypothesis was rejected, it was assumed that a significant and positive relationship could be used to modify the model and improve its performance.

REVIEW OF LITERATURE

HSI Models

Wildlife biologists have been modeling habitat quality for years,
although they might not have used a written model or thought of
themselves as modelers. Daniel and Lamaire (1974) published the
precursor to the type of habitat quality model that is being constructed
today, offering an alternative to the user-day approach to impact
assessment. Using written guidelines, they subjectively determined
habitat values and placed them on a numerical scale between 1 and 10.
Since then, studies comparing approaches to quantifying habitat quality
have demonstrated that use of well-documented, written criteria improves
both accuracy and precision of the outcome (Williamson 1976, Ellis et
al. 1979, Kling 1980, Mule' 1982). This is especially important when
models are used for assessing impacts over time, or any purpose for
which replication of results is desirable.

The first HSI models were compilations of literature with no
guidelines or quality control to direct model content or construction
(N. J. Silvy, pers. commun.). As the use of HEP increased, it became
apparent that the quality of models would have to be improved. A
cooperative demonstration project among the FWS, Soil Conservation
Service, and CE showed both the strength of HEP and the weakness of the
models (U.S. Army Corps of Engineers and U.S. Fish and Wildlife Service
1983).

There has been a growth of sophistication in the development of
habitat models in 2 ways. Models now may be constructed with
intensively collected data and rigorous statistical analysis (e.g.,

Capen et al. 1986), and be expected to perform at the 95% confidence level. If they fail at that level, they are considered useless or dangerous (Byrne 1982, Rice et al. 1986). However, a second attitude is that models can be considered as just another tool for the professional biologist to use (Urich and Graham 1983), and performance at the 70% level is adequate for a model that will be used in planning (Fenwood 1984). Models that perform even more poorly may still have utility (McQuisten and Gebhardt 1983, Salwasser 1986).

HSI and most other habitat quality models are not intended to be models of population dynamics, but hypotheses of the relationship between species and habitat. Although that relationship may be illustrated or exemplified by data on populations, and limiting factors may be identified, cause and effect statements can seldom be made from an application of such models.

Habitat quality models have proven useful for impact assessment, natural area designation (Durham et al. 1988), land use planning (Urich and Graham 1983), and species management (Patton 1984). HSI models are most often applied in the context of HEP, but their utility is not limited to that framework (Wakeley and O'Neil 1988).

The subject of an HSI model may be a species, life stage, group of species, or any other resource of interest for which habitat conditions can be measured. Most models to date have been constructed for species. The output of a HSI model is a value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). Model output should be on a ratio scale so that areas can be compared based on units that are consistent and of known distance apart. This has been translated into an assumption of a

direct and linear relationship to potential carrying capacity, so that
an area with a HSI of 0.6 should support twice as many individuals of a
species as an area that scored 0.3. (In reality, habitat quality should
be twice as high according to whatever measure of habitat is used).
These and other guidelines on models are given in U.S. Fish and Wildlife
Service (1981).

Models are composed of variables that measure the ability of the
habitat to produce the animals' food, cover, water, and other needs.
Variables should use parameters to which the species responds, that are
measurable, whose value can be predicted for future conditions, that may
be affected by the contemplated impact or management action, and that
can be influenced by planning or management decisions (Schamberger and
O'Neil 1986). Variables relating to non-habitat factors beyond human
influence such as weather are usually excluded.

Each variable produces a Suitability Index (SI) on a 0.0 to 1.0
scale, based on a graph that reflects the response of the species to the
parameter measured. The variables are mathematically combined in a
simple equation. Each variable may have a weight that reflects the
modeler's opinion of the relative importance of that factor, with the
default of all variables being equal. Because users may have to modify
a published model to fit their circumstances or region, the
relationships among variables are as straight-forward as possible to
improve user understanding of how the model works.

The geographic area and ecosystem for which a model is built must be
clearly specified. Models for species with large distributions often
must be divided into regions, e. g., following recommendations by Reid

et al. (1977) for Texas. A model is more likely to perform well when it is applied in the realm for which it was constructed. Documentation of a HSI model should include adequate life history information and references to allow a user to decide how well the model might perform. The reason for each variable's inclusion, the form of the graph, and the relationship among variables should be explained. Assumptions on which the model is based, and constraints to its application also are necessary.

Testing HSI Models

Any model, as a simplification of a real system (Hall and Day 1977), must be tested for the degree to which it reflects reality. Its reliability, behavior, and limits must be known before it can be applied with known confidence. Additional and practical reasons for testing a HSI model are to improve its performance and our knowledge of the system being modeled.

A number of published HSI model tests are summarized in Table 1. The table is limited to tests of HSI models for terrestrial species, although tests of other forms of habitat models and of aquatic species are informative. For example, Gaudette and Stauffer (1988) developed a regression model that explained 88% of the variability in white-tailed deer (Odocoileus virginianus) density. Patton (1984) presented a habitat capability model for the Abert squirrel (Sciurus aberti) that produced scores in 5 quality classes from poor to optimum. Squirrel densities over 4 years on 9 plots were correlated with subsequently classed habitats ($r = 0.96$). Soniat and Brody (1988) tested a HSI model for the American oyster (Crassostrea virginica) against population

Table 1. Summary of Published tests of HSI models.

Source	Species	State	Standard of comparison used	Model modified	Sample size	Result
Bart et al. (1984)	Muskrat (Ondatra zibethicus)	La., Oh.	Density from harvest (pelts) in La., from lodges in Oh.	No	15, 24	Neither model showed any statistical relationship to density, but see Cook and Irwin's (1985) reanalysis.
Bayer and Porter (1988)	Pileated woodpecker (Dryocopus pileatus) Downy woodpecker (Dendrocopus pubescens) Veery (Hylocichla ustulata) Black-capped chickadee (Parus atricapillus)	N.Y.	Abundance of each species from survey plots	No	28	Veery and chickadee models predicted 3 classes of habitat, but not on a continuous scale. Woodpecker models unsuccessful in both forms.
Byrne (1982)	Red squirrel (Tamiasciurus hudsonicus) Snowshoe hare (Lepus americanus) Moose (Alces alces) Spruce grouse (Canachites canadensis) Willow ptarmigan (Lagopus lagopus)	Alas.	Expert opinion	Equation only	3-6	Author reported overall failure at 0.05 level, but several subtests were accurate.
Clark and Lewis (1983)	Clapper rail (Rallus longirostris)	Ga.	Abundance from call counts	No	12	Correlations with seasons not significant, r = 0.21 and 0.26.
Clippinger (1989)	Black-tailed prairie dog (Cynomys ludovicianus)	Colo.	Abundance from visual counts	Yes	21	Correlation of r = 0.45 prior to removing 1 variable, r = 0.49 following change.
Cole and Smith (1983)	Eastern phoebe (Sayornis phoebe) Red-eyed vireo (Vireo olivaceous) Prairie warbler (Dendroica discolor) Field sparrow (Spizella pusilla) Meadow vole (Microtus pennsylvanicus) White-footed mouse Peromysus leucopus	W. Va.	Density of each bird species from survey plots, of rodents from traplines, and of rabbits from browse index	Equation only	10	Linear regression r' from 0.48 to 0.65, rank correlation from 0.68 to 0.80.

(Continued)

Table 1. (Continued).

Source	Species	State	Model modified	Sample size	Standard of comparison used	Result
	Eastern cottontail (Sylvilagus floridanus)					
Cook and Irwin (1985)	Pronghorn (Antilocapra americana)	Colo., Id., Mont., Wyo.	Yes	28	Density from censuses	Initial regression explained 39% variability, modification of model explained 50%, model after data transformation explained 70%.
Hammill and Moran (1986)	Ruffed grouse (Bonasa umbellus)	Mich., Wis.	Yes	5	Density from drumming sites	"Mean error of prediction...was 6% below actual field estimates" and the largest measured error was 34%.
Healy (1981, 1983) in Sousa (1985)	Red-spotted newt (Notophthalmus viridescens)	Mass.	Yes	8	Abundance from searches	Final model gave a rank correlation of r = 0.803.
Krohn and Owen (1988)	Common eider (Somateria mollissima)	Me.	No	34	Density of nests	Correlations of r² = 0.69 and 0.58 for HSI with nests/island and nests/vegetated hectare, respectively.
Lancia and Adams (1985)	Pine warbler (Dendroica pinus) Prairie warbler Eastern bluebird (Sialia sialis) Red-cockaded woodpecker (Picoides borealis) Pileated woodpecker	N.C.	No	67	Density from frequency of occurrence at survey plots	Pine and prairie warbler relationships gave r² = 0.87 and 0.93, respectively. No relationships for the other 3 species.
Lancia et al. (1982)	Bobcat (Lynx rufus)	N.C.	No	6,377	Habitat use from telemetry	Significant positive relationship between HSIs and radio fixes; 12% of fixes were in zone of high animal use and low HSI.
Layman and Barrett (1986)	Spotted owl (Strix occidentalis) Marten (Martes americana) Douglas' squirrel (Tamiasciurus douglasii)	Calif.	No	6-201	Habitat use by various methods for the owl and marten, density from cell counts for squirrels	Disappointing overall; with linear tendencies for owl, no relationship for marten and squirrel.

(Continued)

Table 1. (Concluded).

Source	Species	State	Standard of comparison used	Model modified	Sample size	Result
Laymon and Reid (1986)	Spotted owl	Calif.	Habitat use from telemetry	Yes	6 owls	Correlations between individual owl habitat use and 12 best-fit models ranged from r = -0.21 to 0.36.
Mulé (1982)	Caribou (Rangifer tarandus) Beaver (Castor canadensis) Mink (Mustela vison) Spruce grouse Common redpoll (Carduelis flammea) Green-winged teal (Anas crecca carolinensis)	Alas.	Expert opinion	No	Un-known	88% of 192 tests gave mean differences > 0.1, and correlations between HSI values and expert scores were not significant.
O'Meara and Marion (1987)	Cape Sable sparrow (Ammodramus maritima mirabilis)	Fla.	Abundance from survey plots, expert opinion	No	?,49	No relationship between birds and HSI. Expert score correlated with bird numbers and with frequency of occurrence at r^2 = 0.22 and r^2 = 0.87, respectively.
O'Neil et al. (1985)	Field sparrow Pine warbler	Tenn.	Expert opinion	Yes	40	Initial correlation of r = 0.10 increased to r = 0.54 for field sparrow, 0.76 to 0.94 for pine warbler.
O'Neil et al. (1988)	Hairy woodpecker (Picoides villosus)	Tenn.	Expert opinion	Yes	40	Initial correlation of r = 0.07 increased to r = 0.82.

density, modified the model, and achieved an $r^2 = 0.64$.

The degree of success authors reported varies with the final statistics and with the purpose and use of the model. Hammill and Moran (1986:18) stated that their ruffed grouse model still needs improvement but has shown value for management, based on "remarkably good predictions of grouse numbers." Latka and Yahnke (1986) found a value of $r = 0.76$ ($P < 0.0001$) adequate as a prediction of sandhill crane (_Grus canadensis_) habitat use. Mosher et al. (1986) set accuracy criteria at > 80% for tests of models for 2 raptor species. At the other end of the scale, Byrne (1982) and Mule' (1982) found no merit in their results, which included several subtests with close agreement between the model and standard of comparison. Laymon and Barrett (1986) were disappointed in their findings although 2 of their tests produced apparently reliable information.

At least part of the reason for poor results can be determined for some tests. Clark and Lewis (1983) worked with a model that showed little variation in its initial scores, with a HSI for 11 of 12 sites of ≥ 0.92, although the standard of comparison was purposefully and rightly selected for a range of conditions. The authors made no attempt to modify variables or weights or to recalculate scores; they did collect data on candidate variables. O'Meara and Marion (1987) offered several possible explanations for finding no relationships, but O'Meara and Marion (1985) showed all but 1 HSI value to be < 0.3 and noted that modifying the model was not their objective. The initial model described in O'Neil et al. (1988) scored all sites > 0.75, producing a correlation of $r = 0.07$ ($P > 0.50$).

Another problem can be unrealistic expectations, e.g., Mule' (1982) required a distance of 0.1 and $P < 0.05$ for agreement between expert opinion and model scores. In other tests, insufficient information has been reported to determine reasons for poor results, e.g., Bayer and Porter (1988).

Most models perform poorly on their first test and must be modified, based on the test results and/or application at another location or with an independent data set. However, few papers report both testing and modifying models using the test results (see Patton 1984, Cook and Irwin 1985, Hammill and Moran 1986, and O'Neil et al. 1988).

The results of a model test are a function of 4 factors: model subject, content, and structure; data on habitat features; suitability of and data on a standard of comparison; and study design and analysis. Setting optimum conditions for these 4 factors, however, still does not guarantee a successful test (O'Neil and Carey 1986).

Model Subject, Content, and Structure:--Some species are better subjects for models than others. The pine warbler and the prairie warbler, 2 species whose models performed well for Lancia and Adams (1985), were abundant, had relatively small territories, and had habitat requirements that were specific and could be identified. Van Horne (1983:900) identified 3 characteristics of species that "increase the probability that density will not be positively correlated with habitat quality." They are species with social dominance interactions, high reproductive potential, and that are generalists in their habitat requirements. Additionally, species whose life requirements and habitat relations are not well known are more difficult to model.

The more complex the model, the more difficult it is to isolate problems and make changes, or even to interpret results (Bart et al. 1984, Meisel and Collins 1973 in Rexstad and Innis 1985). A large number of variables reduces the sensitivity of each, and increases the chance of interactions which can cloud the test. Inclusion of spatial variables, such as for a species that requires more than 1 habitat type, also increases the complexity of the model. At the same time, if variables are not included that measure critical habitat components, the model can not be expected to reflect habitat quality. Use of variables that relate directly to the environmental features a species requires increases the chance of building a reliable model; indirect measures can introduce error.

Bart et al. (1984) identified faulty model development as the reason for their poor results, i.e., no field data and too little attention given to interactions among variables. Use of an arithmetic mean instead of a geometric mean to combine variables was a positive factor in the test results for Davis and DeLain (1986). Cale et al. (1983) counseled against fitting a model to data or to math and not to ecological processes.

Data on Habitat Features:--Habitat data necessary to run the model must be collected to match the author's definition, e.g., height of the shrub layer, appropriate season for food items, etc. The spatial and temporal scales at which data are collected and at which the species functions (as measured by the standard of comparison) must be the same (Laymon and Barrett 1986, Stauffer and Best 1986). For example, Lancia and Adams (1985) sampled habitat features for pileated woodpeckers on a

grid smaller in size than woodpecker territories. Collecting data and reporting variables in a form that follows a predetermined idea of how the species should respond, e.g., size classes, may bias the model test. Although a model was drafted with the best information on which variables to include and the form of their SI curve, data should be collected on other habitat features that might be important and on a continuous scale so data exist to allow the curves to be redrawn.

Sampling error and inconsistency should be minimized; Gotfryd and Hansell (1985) found high variability of scores among 4 trained observers sampling 20 vegetative characteristics. Half of the measurements were on characteristics commonly used in HSI models.

Standard of Comparison:--Selection of an appropriate standard of comparison has caused the most difficulty and argument in model testing. While many possible standards exist (Downing 1980, Kirkpatrick 1980), population density has become the most commonly used measure, with an assumed direct and positive link to carrying capacity. Both Van Horne (1983) and Maurer (1986) presented a case for using measures of reproductive success, either instead of or in addition to density, to relate to habitat quality. Other standards that may be appropriate include various measures of physiological condition, habitat selection, or expert opinion.

Two major factors confound the use of abundance data as a standard of comparison. First, population levels do not necessarily reflect habitat quality. Population determinants such as weather (Darrow et al. 1981, Hejl and Beedy 1986) may override habitat features. Variation in animal numbers may be explained by considering the scale of measurement (Best

and Stauffer 1986) or stochastic factors (Rotenberry 1986). Van Horne
(1983) provided examples in which density may be higher in low quality
habitat and vice versa because of social interactions. Westmoreland and
Best (1985) found that variables responsible for mourning dove (Zenaida
macroura) nest success were different under conditions of nest
disturbance and non-disturbance. Population levels in many species are
often determined at locations or times of the year other than those that
are the subject of a model, e.g., Fretwell (1968) and Dimmick (1974).
The latter found a correlation of -0.63 between December population
levels and loss of birds from the previous winter. Further, point in
time or short-term population studies only reflect the recent past and
may inadequately reflect long-term abundance; or they may miss an
overriding influence such as poaching.

The second confounding factor is that reliability of population data
is often low or uncertain. For example, some individuals or species
have responses to capture or observation attempts, such as "trap-happy"
small mammals or wary small birds. Harvest data are subject to vagaries
such as a change in hunting effort, weather, or market prices. Some
species experience cyclic changes in densities, both over seasons and/or
years, and such cycles are not always habitat related. In addition,
established techniques for gathering population data may be unreliable
or applied in an unreliable manner. Sources of error include factors
such as observer ability and consistency, weather conditions, animal
detectability, and gear efficiency (Miller 1984).

Using more than 1 standard may just bring more uncertainty. Gaudette
and Stauffer (1988) questioned how well their pellet-group counts

related to deer numbers; counts and state-supplied population estimates were in agreement at only $r = 0.67$. Irwin and Cook (1985) used 2 standards in a pronghorn model test, and found differences between them. Gill (1985) in a study of newt breeding patterns found that using either natality or breeding condition would not be totally accurate at explaining variation. He blamed sampling errors and individual newts who skipped a year in breeding.

Conversely, Rosene and Rosene (1972) found positive and significant correlations among various bobwhite population measurements on 2 plantations in South Carolina, including number of coveys. In Colorado, Snyder (1978) reported several positive relationships. In comparing data from the Ames Plantation and Tall Timbers, Dimmick et al. (1982) reported that the Walk census produced numbers reliably half the size of the Lincoln Index, which was judged to give a true population estimate. Also, Dimmmick (1974:599) wrote "65% of the variation in post-breeding populations was explained on the basis of variations in the total number of nests constructed," with $r = 0.81$.

Study Design and Analysis:--HSI tests are subject to all the expected study design problems. For example, sample size should be adequate for the rigor of test desired (Marcot et al. 1983); O'Meara and Marion (1987) thought this might be a weakness in their test.

An adequate and complete range of habitat conditions, expressed as variables, must be measured to avoid misleading relationships (Green 1979, Meents et al. 1983). If a study area is homogeneous, the model may not differentiate among sites and so provides little information. A range of apparent habitat quality also is necessary to allow the model

to be tested to its limits.

The type of statistical analysis may affect the test results; e.g., Meents et al. (1983) found that linear relationships between bird population densities and habitat variables were most common, but that a significant curvilinear relationship was seen a third of the time. Even worse, the relationship changed from linear to nonlinear with the changing of a season for some species.

Intercorrelated variables commonly occur in habitat studies. When predictor variables are multicolinear, switching of variables can occur and cause problems in interpreting the importance of the predictor variable (Green 1979). Mosher et al. (1986) omitted 1 of each pair of variables with a correlation of > 0.7, Morrison et al. (1987) used 0.8 as a cutoff. However, Irwin and Cook (1985) did not remove intercorrelated variables to keep the model more robust. Gore (1986) maintained some highly correlated pairs because he thought they represented distinct ecological features to the small mammals in his study.

Some researchers have advocated testing the entire model, and others focus on its components. Evaluation of components of a model can successfully build toward a more accurate and useful model (Cale et al. 1983). Therefore, when the HSI scores do not agree with scores from the standard of comparison, analyses of internal portions of the model may locate the reason for the discrepancy (O'Neil et al. 1988). For a HSI model, that includes assumptions, variables, curves, mathematical relations, interim output, and final output.

The end result must be viewed in an appropriate context, i.e., a

validated model being tested under rigorous conditions should be expected to produce higher correlations than a new model tested with one season of data or with a standard of comparison low in reliability. Likewise, if a model is only required to rank sites for relative habitat quality, a less rigorous test will be acceptable. Alpha levels are traditionally set at < 0.05, but higher levels may be appropriate for some purposes. McQuisten and Cebhardt (1983) suggested the use of < 0.15 for general purposes, land use decisions, etc., excluding litigation. Levels < 0.25 were suggested for reports, with qualifications. Levels > 0.25 may still be useful for information.

Finally, interpretation should include the purpose of a test. For example, with hypothesis testing, acceptable test results do not verify a model, they fail to inval date it. However, while testing a model to meet an objective, acceptable test results will verify the model for its intended use.

Habitat Quality for the Northern Bobwhite

The bobwhite is a good subject for an HSI model. Although some may argue that there is never enough, adequate data exist on the relationship between quail populations and measurable features of the environment to allow model construction. Population levels are heavily influenced by habitat quality, allowing a direct link between excellent habitat and high populations. The bobwhite is a popular animal, often selected as a species for use in an impact assessment or management plan. The bobwhite responds to changes in land use practices and is therefore able to act as an indicator of impacts from some types of human activities.

A difficulty in the modeling process is the widespread distribution of the bird, with a correspondingly wide variation in weather and climate conditions and in plant species for food and cover. The modeler must either incorporate non-specific features or reduce the geographic applicability of the model to some portion of the bobwhite's range. Another difficulty arises in locations or times in which the direct link between habitat and populations is overridden by non-habitat influences. For instance, predation may play a larger role under conditions of habitat loss or deterioration (Errington 1934, Klimstra 1982).

The 2 primary determinants of bobwhite density are annual recruitment and overwinter mortality (Klimstra and Roseberry 1975). On that basis, the major habitat-related limits on a bobwhite population are food and nesting and brood cover in the breeding season, and food and escape cover in the winter. Food must be available, palatable, nutritious, and small enough for ingestion. Cover must be adequate for the seasonal needs, and in proximity to an adequate food supply. The following review highlights these factors as they relate to a HSI model.

Food:--Food habits of the bobwhite have been studied extensively. Most studies have found a clear dominance of plant material, especially seeds, across the range of the bird (Handley 1931, Larimer 1960, Eubanks and Dimmick 1974, McRae et al. 1979, Wilson 1984, Campbell-Kissock et al. 1985). The relatively small list of species or food groups eaten in each locality indicates feeding selectivity. McRae et al. (1979) in Florida found 22 plant foods provided 97% of the food eaten by 185 birds; an additional 45 foods were recorded. Landers and Johnson (1976) summarized 27 food habit studies conducted in 10 states of the southeast

between 1931 and 1972 (n - 19,347), and found 45 seed foods "to be repeatedly selected by quail." In Illinois, Larimer (1960) analyzed 4,171 crops during the hunting season and recorded only 14 plant foods that comprised a volume greater than 1%; 8 of those were found in at least 10% of the crops. Nearly half, by volume, of the plant foods in 672 Tennessee birds were soybeans (Eubanks and Dimmick 1974).

Analysis of food items during the entire year sometimes provides a different picture. Factors affecting variation in feeding include age, sex, and season of year (Stoddard 1931, Eubanks and Dimmick 1974, Roseberry and Klimstra 1984). Berries were important both to juveniles and to all birds during dry periods (Stoddard 1931). In feeding trials of chicks between 2 and 15 days of age in Mississippi, both seeds and insects were selected, although younger chicks ate more insects than older chicks (Hurst 1972). Wilson (1984) found significant differences in the percent volume of 4 food types (grass, forb, woody, and animal) between breeding and nonbreeding seasons in 120 birds in south Texas. Eubanks and Dimmick (1974) found that summer diets of females were 36.2% by volume animal food; the males ate 19.9% animals. Juveniles until the age of 7-9 weeks relied heavily on animal foods. In Indiana, Priddy (1976) found animal matter first in frequency of occurrence at 31.2% in 401 birds over the fall and winter. Occurrence by volume was comparable to other studies, however.

Although selectivity for food has been documented with a relatively small set of plant species or groups being dominant, high quality habitat contains a variety of potential foods to allow dietary shifts. In addition to shifts related to changes in bird age or season, weather

conditions can cause a change in diet. Dimmick (1974) recorded a warm winter during which soybeans sprouted and deteriorated, and the birds moved to the timber to eat sweetgum (_Liquidambar styraciflua_) seeds. McRae et al. (1979) recorded a shortage of legumes and other seed-producers in Georgia because of drought, with a consequent shift in bobwhite preference to acorns. Landers and Johnson (1976) called the 45 most important seeds "staple food" with another 33 species buffer foods that may become important under different conditions. Other events such as ice or snow cover (Snyder 1978) or change in cropping practices can alter the foods available and therefore eaten.

The presence of a variety of potential foods also compensates for differential quality of seeds over winter. Larimer (1960) and Preacher (1977) found highly variable degrees of soundness in their samples, both within and across species, and presumably wide variation in nutrient content. Not all foods a bobwhite eats can provide sufficient energy to assure survival; e.g., soybeans are a common food, although Robel and Arruda (1986) found that they rank low in usable energy content. Gluesing and Field (1986) referred to their earlier work that estimated how much of the daily minimum nutritional requirements 24 important foods provided for bobwhite; half the food items lacked the ability to support quail over the winter. Habitat that supplies a variety of forms of food will improve the chances of bobwhite obtaining adequate nutrients.

A comparison of the most important food items in several studies over a large part of the bobwhite range shows similarities. Of the 45 items in the Landers and Johnson (1976) review, 37 are common to all 4 regions

represented in the survey (Coastal Plain, Piedmont, Plateau, and Mountain). Another 5 are common to all but the Mountain area. All of the top 14 plant groups in Illinois (Larimer 1960) are included within the 45 foods listed by Landers and Johnson (1976). Larimer also reviewed studies from Indiana, Missouri, and Pennsylvania (states not included in Landers and Johnson [1976]) and found considerable agreement in importance of 9 of his 14 foods. Fifteen of the 24 "principal species of seeds" in Bookhout's (1958) study in Illinois match the 45, and 2 others share a genus. Six plant species or groups predominant in studies by both Wilson (1984) and Campbell-Kissock et al. (1985) are found in the Landers and Johnson's 45.

There are differences, however, in parts of the bobwhite range. The 2 Texas studies had 6 species or groups in common with Landers and Johnson's list, but 4 and 43 food items, respectively, were not (Wilson 1984, Campbell-Kissock et al. 1985). In Colorado, 5 of the 9 food items comprising > 20% occurrence over 1-3 years were included in Landers and Johnson's 1976 list, and most of the lesser occurring foods were not included. Landers and Johnson (1976) excluded studies from south Florida because foods were nearly unique to the locality; this also may be true of Texas. Larimer (1960) cited large differences between his Illinois and 2 Oklahoma studies.

More studies report food preferences by volume than frequency although Landers and Johnson (1976) combined both into an importance value. When I had a choice in interpreting a study, I relied on frequency information as being a better reflection of food availability over the long-term. Volume is more dependent on a chance find (e.g.,

termites cited in Wilson 1984) and size of the food item.

As recorded in the food habit studies cited above, foods eaten by the bobwhite include agricultural products, wild grass and forb seeds and vegetation, hard or soft mast, and animal material. Agricultural lands provide both the seed of the crop as well as grass and forb seeds and vegetation if agricultural practices are appropriate, either in crop residue, remaining stubble, or along the edges of the field. Corn, soybeans, sorghum, and wheat are the primary crops eaten.

Grasses and forbs that form the early stages of succession are of major importance and most numerous in species. They are found associated with croplands; in fallow and idle fields; in woodland openings; as understory in woodlands; and along roadsides, fencerows, and other disturbed areas. Of the 27 staple foods in Landers and Johnson (1976) that are grasses or forbs, 13 (excluding soybeans and black locust) are legumes.

With regional variation in amount, the most frequently eaten mast species are oak (_Quercus_ spp.), sumac (_Rhus_ spp.), pine (_Pinus_ spp.), dogwood (_Cornus florida_), sweetgum, black locust, sassafras (_Sassafras albidum_), ash (_Fraxinus_ spp.), grapes (_Vitus_ spp.), and blackberry (_Rubus cuneifolius_). Other mast such as black cherry (_Prunus serotina_) and hackberry (_Celtis occidentalis_) have been locally or seasonally critical (e.g., McRae et al. 1979, Campbell-Kissock et al. 1985).

Animal foods eaten by quail include a variety of invertebrates, with Orthopterans and Coleopterans most often cited. The smaller organisms are especially important for the young (Hurst 1972). Additional orders represented include Pulmonata, Isoptera, Hemiptera, Homoptera,

Lepidoptera, Diptera, Hymenoptera, and Araneida (Hurst 1972, Wilson 1984, Campbell-Kissock 1985, Jackson et al. 1987). When vegetation exists as described above for non-woody areas, adequate invertebrates also are assumed present.

Appropriate food must be available, as well as present. Several authors refer to the need for incomplete cover of vegetation to allow quail to move freely to feed, and no or only a light litter layer so birds can reach seeds lying on the soil surface (e.g., Stoddard 1931, Hurst 1972, McRae et al. 1979). Dense grass also may limit output of more productive food plants (Kiel 1976).

Nesting and Brood Cover:--Nests are placed on the ground in or near clumps of grass, pine straw, or other vegetation occurring on the site (Klimstra and Roseberry 1975, Simpson 1976). Nests are constructed of vegetation in the vicinity, primarily dead grasses of the previous season. Of 1,052 items used in nest construction in Klimstra and Roseberry's (1975) study, 88% were grasses, and grasses provided cover for 70% of the nest sites. Woody vegetation was present at over half the nest sites. In areas with regular controlled burning, nests are often in clumps of the previous year's vegetation (Simpson 1976). However, burning may provide variable nesting cover (Dimmick 1971), because of changes in burning frequency, fuel, weather, etc.

Rosene (1969) thought that optimum vegetation height should be less than 51 cm. Klimstra and Roseberry (1975) found an average vegetation height of 49.5 cm around 317 nests.

Vegetation density in the vicinity of the nest is relatively low. Simpson (1976) characterized it as medium or sparse (some bare ground

between clumps or around the majority of the plants) in 83% of 2,759 nests. Average basal area of vegetation within 1 m of the nest was 8%, with a range of 1 to 25%. Harshbarger and Simpson (1970) measured average herbaceous cover around nests at 48%, with a range of 10 to 85%. Areas with < 21% shrub cover within 1 m of the nest were preferred.

Both Stoddard (1931) and Rosene (1969) stressed the importance of open space within and under vegetation for nesting preferences and ease of movement. Of 31 nests located by Minser and Dimmick (1988), 11 were in no-till crop fields that probably included a considerable amount of bare ground from cultivation and dead grasses from herbicides. The others were located in idle fields and fence rows, with 1 in a wheat field. Idle fields and roadsides supported the most nests in Illinois (Klimstra and Roseberry 1975), with an open aspect, access to bare ground, and non-rank vegetation considered to be important. These conditions may be found in a variety of habitats, including parcels with old field succession, rangelands, and pine plantations.

Nests on low ground are less productive than those on higher ground because of the danger of spring floods or puddles. In Klimstra and Roseberry's (1975) sampling, drainage was excellent to good in 76.3% of 1,009 nest sites. Errington (1933) found 80% of 69 nests at sites with excellent to good drainage.

Brood habitat was described in Texas by Cantu and Everett (1982:82) as "grassy, weedy areas of sparse to medium density with 15-70% bare ground." They found broods avoided dense cover, i.e., > 85%. For cover from heat, they used brushy areas with very sparse understory.

Spatial Relations:--Bobwhites are generally considered edge species

and require a diverse environment on a small scale to meet food and cover requirements during the year (Rosene 1969). If its needs can be met, a bird may move only a short distance over its lifetime. For example, 98% of 676 quail studied over 10 years in northern Florida moved no more than 800 m, and 88% moved < 400 m (Smith et al. 1982). Simpson (1976) showed 92% of quail movements within a year to be < 400 m and 98% < 800 m. Other researchers have recorded movements of longer distances and considerable variation within a year where suitable patches of habitat were not compactly arranged or where other aspects of habitat quality were low (Urban 1972, several citations in Smith et al. 1982, Roseberry and Klimstra 1984). Bell et al. (1985) studied quail in unmanaged pine plantations; range sizes and daily distance movements apparently increased with decreasing habitat quality, expressed as coverage of food plants.

Stoddard (1931) found 74% of about 600 nests within 15 m of openings. Klimstra and Roseberry (1985:17) located almost 60% of 707 nests "within 5 m of a noticeable break in the cover pattern." In Georgia, 58% of 1,311 nests were within 3 m of an opening (Simpson 1976), although the author noted that openings were frequent. Radioed hens with broods were always located within 10 m of breaks in vegetation in Texas (Cantu and Everett 1982). In Louisiana, Bell et al. (1985) recorded 53% of 180 telemetry fixes within 50 m of some edge. Hanson and Miller (1961) found the number of fall coveys and occurrence of 2 forms of edge correlated at r = 0.973.

The type and distribution of the various cover types that meet quail needs will vary with land-use conditions, so prescriptions for habitat

composition are difficult to determine. In addition, contiguous habitat types influenced quail use of forest land in Louisiana (Bell et al. 1985) and Illinois (Klimstra and Roseberry 1975). Rosene (1969) suggested that grazing land should be less than 20% of an area, and recommended a 50:50 ratio of woody and non-woody vegetation. Leopold (1933) recommended equal proportions of woodland, brushland, grassland, and cultivated aras. The extent of suitable nesting habitat must be great enough to allow both unused and repeated nest building (Klimstra and Roseberry 1975).

Reid et al. (1977) examined the relationship between call counts and cover types in 9 ecological areas of Texas, finding few clear patterns except differences among the areas. Wiseman and Lewis (1981) in Oklahoma found tall and short shrubland types first and second in quail preference, serving as areas for feeding, resting, and escape cover. Quail studied by Bell et al. (1985) selected clear cuts, bottomlands, and associated edges. Snyder (1978) found coveys concentrated near edges in Colorado, feeding in winter in early successional vegetation with adjacent cover. The most important cover type was forb-dominated river banks periodically scarifed by water. Areas with more shrubs and grasses were less used. In Tennessee, Exum et al. (1982) performed regression analysis on population numbers and several land-use categories. Results included positive correlations with pastures and idle land and negative correlation with soybeans (r = 0.76. 0.76. and - 0.63, respectively). If one were to construct a model using their data and results, the variables would be centered around idle land, comprised of both woody and herbaceous vegetation. Minser and Dimmick (1988)

summarized winter cover type needs as crop lands, idle fields, fence rows and thickets, and woodlands.

Interspersion of cover types is critical. Use of grassland "occurred within 200 m of woody habitats" in Colorado rangeland (Wiseman and Lewis 1981). The number of cover types and coveys were correlated in Illinois at r = 0.981 (Hanson and Miller 1961). Baxter and Wolfe (1972) compared audio census results with calculation of interspersion of cover types in 3 counties of Nebraska and found a strong relationship (r = 0.976). Priddy (1976) reported similar results (r = 0.936) for interspersion and call counts on 3 census routes in Indiana. He also reported no relationship when the analyses were run on individual stops along the routes, and r = -0.664 with call counts and an alternative way of calculating interspersion. In Texas, a measure of interspersion was significantly correlated with call counts in 5 of 9 areas, with r = 0.55, -0.60, and 0.80 (Reid et al. 1977).

Other Habitat Factors:--Other requirements include adequate escape and refuge cover, well-drained roosting sites, sufficient drinking or metabolic water, and dusting sites (Rosene 1969). Escape cover can be provided by a stand of trees with low branches, thick and tall grass, or shrubby vegetation such as fence rows and gullies. Yoho and Dimmick (1972) and Roseberry and Klimstra (1984) found honeysuckle (Lonicera japonica) in woodlands important as escape cover.

Roosting habitat was characterized by Klimstra and Ziccardi (1963) as having a bare or nearly bare ground surface, short and sparse vegetation, and an open canopy. Pastures and other grassy cover types are probably most used for roosting (Wiseman and Lewis 1981, Roseberry

and Klimstra 1984) although Rosene (1969) and Wiseman and Lewis (1981) recorded roosts in open woodlands and shrubland, respectively. Yoho and Dimmick (1972) linked honeysuckle to roost sites. Cantu and Everett (1982) found broods roosting in areas with 80% bare ground.

Prasad and Guthery (1986) observed bobwhite drinking at a reservoir, and related that behavior to limited availability of water from foods and to higher temperatures in south Texas. Reid et al. (1977) found no particular relationship between bobwhite populations and the presence of water. Under most conditions, free drinking water is not thought to be necessary (Stoddard 1931), at least in the southeast.

Dusting sites are small patches of mostly bare ground, often found at roadside or in sparse, short vegetation (Rosene 1969). While dusting and each of the other habitat factors discussed can become critical to bobwhite survival and should be considered in management, they are nearly always provided by conditions that provide adequate food and nesting or brood cover. As defined in the HSI model, for example, a variable for the coverage of light litter or bare ground is included to provide open ground surface for feeding and ease of movement; that also will provide dusting sites.

Spatial Calculations

The relatively sedentary bobwhite requires habitat features most often found in more than 1 cover type, at least as defined by humans. It is generally true that higher habitat quality is found on sites in which appropriate cover types are found intermixed with each other over a small area. This would be called juxtaposition by Giles (1978), although interspersion has been more often examined in the literature.

Although both are important, the bobwhite appears to be affected more by habitat structure than by species composition. This leads to the possibility of a short cut to determining habitat quality, based on concepts such as edge, interspersion, and juxtaposition.

An index of interspersion of habitat types was presented by Baxter and Wolfe (1972) for quail in Nebraska. They defined distinct cover types within audio distance of census routes, overlaid a grid of diagonal lines on aerial photos of the area, and counted the number of times 1 cover type changed to another along the lines. The changes were summed for each of 3 counties, and their absolute numbers compared with census results. Priddy (1976) reported use of 2 versions of Baxter and Wolfe's (1972) index. When the index was calculated along diagonal lines, the correlation between call counts and interspersion was 0.936. When interspersion was calculated along radial lines from the sample point, r - -0.664. He did not explain the difference.

Fried (1975) and Patton (1975) suggested application of a measure of the irregularity of a perimeter as an index of edge, translated to degree of interspersion. Their index was related to an increase in edge over that of a circle, but independent of the size of the area being measured. Patton's application included a larger measure of perimeter by adding internal borders.

Taylor (1977) compared indices derived from the previous 3 methods and found a significant correlation (r - 0.985, n - 11, P <0.001). He pointed out their lack of statistically-established relationship to wildlife populations. He also described Fried and Pattons' indices as identical, which is not apparent from their writing. Taylor found the

Baxter and Wolfe approach easier to use overall, but suggested the other 2 might be easier on small odd-shaped parcels.

McCall (1979) described a method to determine and portray suitability of vegetative cover for selected species, including bobwhite, using an air photo overlain by a clear plastic scale with home ranges delineated. The user applies criteria for cover to land within the home range and assigns a score. The author presented criteria for Indiana as an example and recommended that others be developed by local interdisciplinary teams.

A method of calculating interspersion, juxtaposition, and spatial diversity to evaluate habitat potential was presented by Heinen and Cross (1983). Changes in defined cover types are counted as in Baxter and Wolfe (1972), but instead of a summation, the position of each grid cell is mathematically described in relationship to each other. Spatial diversity is determined by an equation that combines interspersion, juxtaposition, and modifiers for positive or negative factors pertinent to a particular species.

STUDY LOCATION

The Ames Plantation consists of 7,500 ha located 80 km northeast of

Memphis, Tennessee, in Fayette and Hardeman counties (Fig. 1). The

nearest town is Grand Junction, 4 km southwest of the plantation. Since

1950, the land has been managed by the Hobart Ames Foundation to provide

research and education opportunities for the University of Tennessee

(UT). It also is the site of the National Field Trial Championships for

bird dogs.

Land management practices in agriculture and forestry are largely

conducted for the benefit of the northern bobwhite. Cover types on the

plantation are well interspersed and include hardwood and pine timber

stands, savannas, old fields, pasture, grasslands, and croplands. Plant

species are typical of the Bailey (1980) Oak-hickory Forest Section,

Number 2215, with the addition of loblolly pine (Pinus taeda) and

shortleaf pine (P. echinata) plantings. Crops include soybeans and

corn, and supplemental plantings of bicolor lespedeza (Lespedeza

bicolor) are placed in the timber.

Because of the close affiliation of the plantation and university,

extensive research on bobwhite natural history, habitat requirements,

and response to management has been conducted (e.g., Eubanks 1972, Yoho

and Dimmick 1972, Minser and Dimmick 1988). These and other studies

have included census data from 1966 to the present (R. D. Dimmick, pers.

commun.), and quail populations as compared to land use practices over

time (Exum et al. 1982).

The Ames Plantation is located at latitude 35 05' and longitude 89

15'. The area receives 135 cm of precipitation a year on the average,
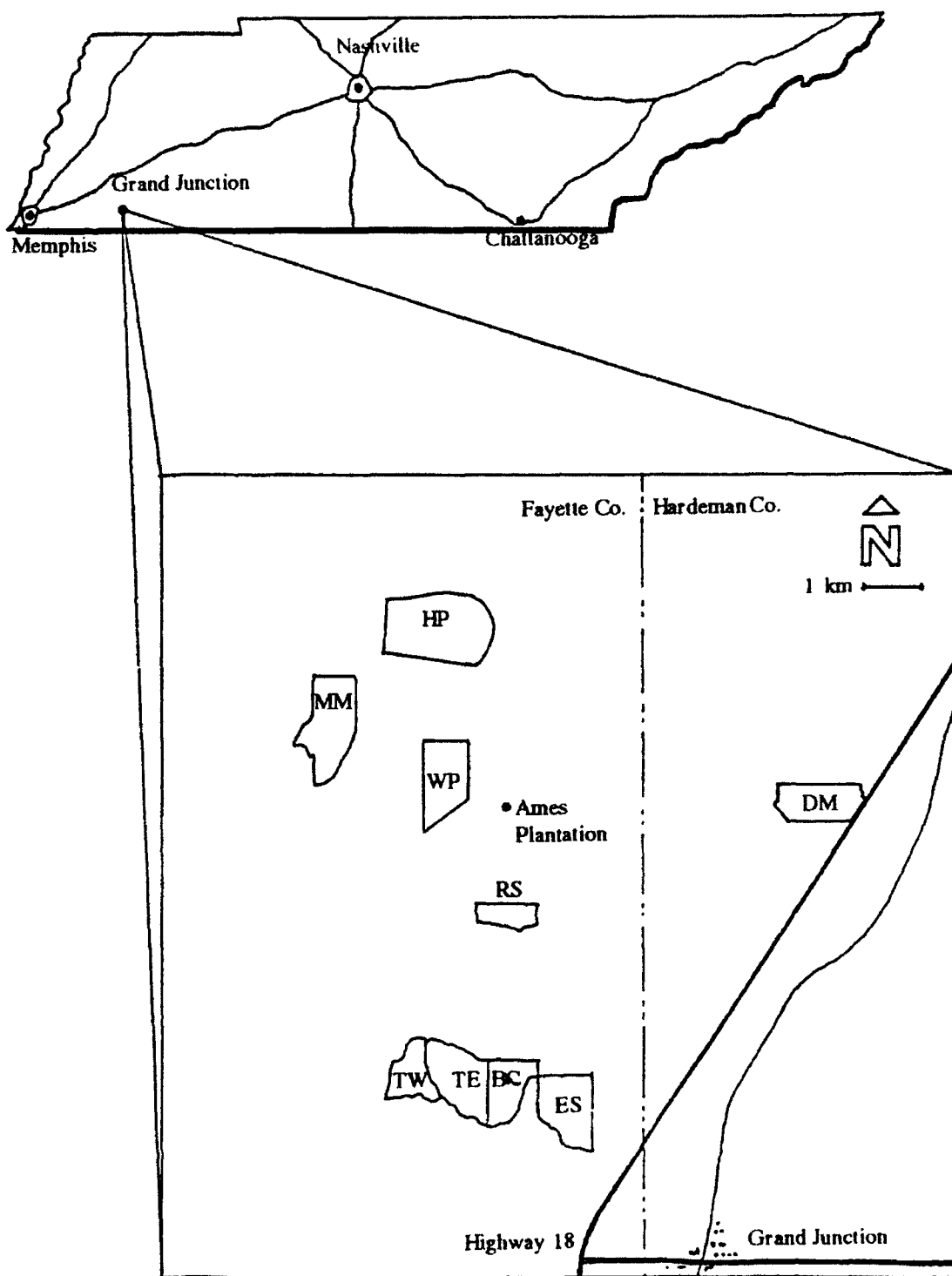
Fig. 1. Location of Ames Plantation and 9 study areas used in test and modification of the draft bobwhite HSI model (Schroeder 1983), Grand Junction, Tennessee.

with the wettest month January and the driest month October. Average annual snowfall is 11.7 cm. Average temperature is about 16 C, with the highest monthly mean of 27 C occurring in August and the lowest monthly mean of 6 C in January. Number of annual frost-free days is 200, occurring between 2 April and 24 October (U.S. Department of Agriculture 1964).

A soil survey for Fayette County (U.S. Department of Agriculture 1964) provided the following information. All but 1 study area (Demo Farm) are covered by this survey. The topography is moderately rolling with average elevation on the study areas between 137-171 m above sea level. The soils are Coastal Plain marine sediments overlain by air-blown loess, which is about 2 m thick in eastern Fayette County. The Plantation is in the Loring-Memphis-Lexington-Ruston Association. The soils are a mosaic of series, but mostly silt loams with 0-5% slope. There are numerous drainages with slopes to 12%. The most common series on the study areas used in this research is Memphis, which is well- to moderately well-drained and naturally fertile. The second most common classification is Gullied lands, formerly Memphis, Loring, or Grenada soils. Memphis soils are now mapped as Lexington (R. J. Creel, pers. commun.)

Study Area Descriptions

Nine study areas were delineated, with 7 selected because of their use by UT researchers. Two were added to expand the range of conditions for a model test to include habitat on the low end of a quality scale. Fig. 1 shows the location of each study area.

Table 2 provides the size of each study area and vegetation cover

Table 2. Summary of sizes and vegetation components of bobwhite study areas on the Ames Plantation, Grand Junction, Tennessee, in August-September 1983. Units were defined by breaks in dominant plant cover.

Study area name	Acro-nym	Area size (ha)	All cover type units				Deciduous forest (DF)[a]					Deciduous shrub (DS)				
			No.	No. units/ha	Mean size	Median size	Extent (ha)	No. of units	% of area	Mean size	Median size	Extent (ha)	No. of units	% of area	Mean size	Median size
Billy's Covey	BC	55.4	52	0.94	1.06	0.38	14.29	10	25.8	1.43	0.93	2.67	12	4.8	0.22	0.12
Demo Farm	DM	73.7	19	0.26	3.88	0.20	17.73	3	24.1	5.91	7.77	0.61	9	0.8	0.07	0.04
East Side	ES	67.2	53	0.79	1.27	0.36	34.52	9	51.4	3.84	0.40	1.98	12	2.9	0.17	0.06
Hancock Pasture	HP	130.8	52	0.40	2.51	0.24	56.74	8	43.4	7.09	4.52	3.20	13	2.4	0.25	0.20
Martin McKinney	MM	96.5	40	0.41	2.41	0.18	53.66	4	55.6	13.42	3.65	2.43	9	2.5	0.27	0.14
Rube Scott Road	RS	34.7	25	0.72	1.39	0.53	11.82	3	34.1	3.94	0.69	0.53	4	1.5	0.13	0.08
Turner Ditch East	TE	56.3	66[b]	1.17	0.85	0.26	5.10	5	9.1	1.02	0.67	17.36	30	30.9	0.58	0.12
Turner Ditch West	TW	56.2	36	0.64	1.56	0.16	14.57	4	25.9	3.64	3.10	0.36	7	0.6	0.05	0.04
West Pasture	WP	62.5	28	0.45	2.23	0.43	22.74	4	36.4	5.69	4.09	1.38	12	2.2	0.11	0.04
Totals		633.2	371				231.17	50				30.52	108			

[a] There were 4.78 and 16.19 ha of Evergreen Forest delineated on areas MM and WP, respectively; they were included in the Deciduous Forest classification.

[b] An additional 20.40 ha of Tree Savanna were delineated on area TW and sampled separately.

Table 2. Extended.

Forbland (F)					Grassland (G)					Pasture/Hayland (PH)					Cropland (C)				
Extent (ha)	No. of units	% of area	Mean size	Median size	Extent (ha)	No. of units	% of Area	Mean Size	Median Size	Extent (ha)	No. of units	% of area	Mean size	Median size	Extent (ha)	No. of units	% of area	Mean size	Median size
6.88	20	12.4	0.34	0.22	2.87	1	5.2	2.87	2.87	0	0	0	0	0	28.69	9	51.8	3.19	3.44
2.15	3	2.9	0.72	0.81	0	0	0	0	0	53.18	4	72.2	13.29	8.30	0	0	0	0	0
6.60	19	9.8	0.35	0.28	1.90	2	2.8	0.95	0.80	0	0	0	0	0	22.18	11	33.0	2.02	1.38
16.19	13	12.4	1.25	0.08	7.00	8	5.4	0.88	0.08	9.83	4	7.5	2.46	1.98	37.80	6	28.9	6.30	5.28
2.23	6	2.3	0.37	0.08	3.48	13	3.6	0.27	0.12	0	0	0	0	0	34.72	8	36.0	4.34	3.81
2.47	9	7.1	0.27	0.14	1.17	3	3.4	0.39	0.28	18.70	6	53.9	3.12	2.61	0	0	0	0	0
11.17	14	19.9	0.80	0.43	1.38	9	2.5	0.15	0.06	0	0	0	0	0	21.25	8	37.8	2.66	2.74
10.73	11	19.1	0.98	0.16	0	0	0	0	0	0	0	0	0	0	10.16	13	18.1	0.78	0.16
3.40	6	5.4	0.57	0.51	1.05	2	1.7	0.53	0.53	2.67	1	4.3	2.67	2.67	31.24	3	50.0	10.41	11.86
61.80	101				18.85	38				83.38	17				186.04	58			

types identified. Soil descriptions for all but 1 study area were taken from U.S. Department of Agriculture (1964); information for the Demo Farm was obtained from the Soil Survey Office mapping Hardeman County in 1988 (R. J. Creel, pers. commun.).

The number of cover type units ranged from 19-66, with an average size of < 4 ha on all areas, and a median size of 0.53 ha or less. All areas had deciduous forest, deciduous shrubland, and forbland. Two lacked grassland, 2 lacked cropland, and 5 lacked pasture/hayland. A short description of each area follows.

Billy's Covey (BC) has 5 well-interspersed cover types, with half of the area in cropland and another quarter in deciduous forest. Soils are primarily silt loam of the Loring Series and secondarily Henry. Grenada and Collins silt loams also are represented. Slopes are 2-5% with a ridge that reaches 8%. The composition of cover types on 3 sides of BC is similar to its internal composition, with roads bordering those 3 sides. The fourth side is primarily unbroken forest.

Demo Farm (DM) is 72% pasture in 4 large blocks and 24% deciduous forest; the remainder is in forbland and deciduous shrubland. It is the least diverse in pattern of cover types. The area contains a farmhouse and related structures. DM is bounded on 2 sides by forest and on the other 2 by cropland and pasture. Soils are nearly all Lexington (formerly Memphis), with a small percentage of Loring.

East Side (ES) has a large block of deciduous forest occupying half the study area, but cover types in the western third are highly interspersed. A third of ES is in cropland. Silt loams of Loring and Memphis, Vicksburg fine sandy loam, and Gullied sand are well

interspersed. Of secondary abundance are Collins and Henry soils, plus representatives of another 3 series. Slopes are 0-5% with 3 areas of Memphis silty clay loam to 8% slope. Adjacent cover types are similar except the east side which is a large block of cropland and the northeast which is forest.

The largest area is Hancock Pasture (HP). It is surrounded by largely unbroken forest, but its 6 cover types are moderately well interspersed. Deciduous forest is the predominant cover type with cropland second in extent. The largest extent of forbland on all study areas is on HP. Soils are well interspersed, with the most common being Memphis and Loring silt loam and Gullied sand and silt. Five other series also are present. Slopes are 0-5%.

Martin McKinney (MM) is 56% deciduous forest and 36% cropland, with cover types in large blocks in the north part of the area. Adjacent lands to the east are forested; there are multiple cover types on the other sides. The most common soil is Memphis silt loam, with Henry, Callaway, Grenada, and Gullied silts and sands intermixed. There also are units of 7 other series. The eastern side has a partial border of Ruston sandy loam with 12-30% slope. The remainder of the area has a slope of 0-5%.

The smallest area, Rube Scott Road (RS), has all cover types moderately well interspersed but the largest median unit size. RS is 54% pasture and 34% deciduous forest. The area is bounded on the north by forest, on 2 sides by crops and roads, and on the west by forest and an orchard. The most common soils are in the Collins (fine sandy loam) and Memphis series; silt loams of Lexington and Grenada, fine sandy loam

of Waverly, and 3 other series also exist. Slope is generally 2-5%.

Turner Ditch East (TE) is highly interspersed with 31% of the area in deciduous shrubland, 38% in cropland, and 20% in forbland. It has the most diverse pattern with the highest number of units and the lowest mean size of a cover type unit of any area. Adjacent lands have similar cover types and are equally well interspersed. The area is dominated by Gullied sand and Grenada silt loam. There also is a considerable amount of Calloway, Henry, and Loring silt loams. The steepest slope is 5%.

Turner Ditch West (TW) has a 20-ha central block of evergreen and deciduous tree savanna, but the other two thirds of the area is moderately well interspersed with deciduous forest, forbland, and cropland. The median size of its units (0.16 ha) is the smallest of any study area. Land to the south is forested, to the west is cropland, and the rest is a mixture of types. There is no dominant soil type, but a mixture of Calloway and Grenada silt loams, Gullied silt and sand, Collins silt loam, and a Loring-Gullied land complex. The latter has slopes of 8-12%, the rest of the area has 2-5%.

West Pasture (WP) is half cropland in 3 blocks and a third deciduous and evergreen forest, with moderate interspersion. Adjacent lands are similar. Soils are primarily Memphis silt loam, and secondarily Lexington silt loam, silty clay loam, and sandy and silty Gullied land. A 2-8% slope is present.

METHODS

Overview

Two sets of analysis were performed. The first compared scores from a habitat quality model for the northern bobwhite with census data on 9 study areas. The second compared selected spatial measurements with the census data and a modification of the model.

Scores or ratings to use as a standard of comparison for the model were obtained by converting data from the bobwhite census to an index. Model scores were calculated by measuring variables on each study area, converting the data to SIs, and calculating the HSI. Relationships between the 2 sets of scores (standard of comparison and model) were then analyzed to determine if model output was positively related to bobwhite numbers. The internal outputs of the model were then analyzed to determine changes to the model that would improve its correspondence with population numbers.

Draft Model

The bobwhite habitat quality model examined was a draft HSI model authored by Mr. Richard Schroeder of the FWS (Table 3 and Fig. 2). It was based on literature and on review comments of 9 people considered experts on bobwhite habitat. It received no prior test.

The model was constructed for the bobwhite's range in the eastern U.S. and for all cover types in that portion of the range. It evaluates habitat quality on the basis of 3 Life Requisites: food, nesting, and cover; and incorporates interspersion factors to accommodate the species' requirement for more than 1 cover type.

Table 3. Variable number and variable name from the draft bobwhite HSI model (Schroeder 1983) tested on the Ames Plantation, Grand Junction, Tennessee; and abbreviated variable names used in text.

Variable number	Identification of variable	Abbreviated name
1	Percent canopy cover of preferred bobwhite herbaceous food plants	Food plants
2	Percent of ground that is bare or covered with a light litter	Bare ground
3	Type of crop present	Crop type
4	Overwinter crop managment	Crop managment
5	Percent canopy closure of pine or oak trees > 25.4 cm dbh	Mast
6	Percent cover of shrubby and other woody vegetation in the height zone < 2 m	Cover
7	Percent grass canopy closure	Grass percent
8	Average height of grass canopy	Grass height
9	Soil moisture regime	Soil moisture
10	Percent area in equivalent optimum winter food	Optimum food
11	Percent area in equivalent optimum cover	Optimum cover
12	Percent area in equivalent optimum nesting habitat	Optimum nesting
13	Distance between cover types	Distance
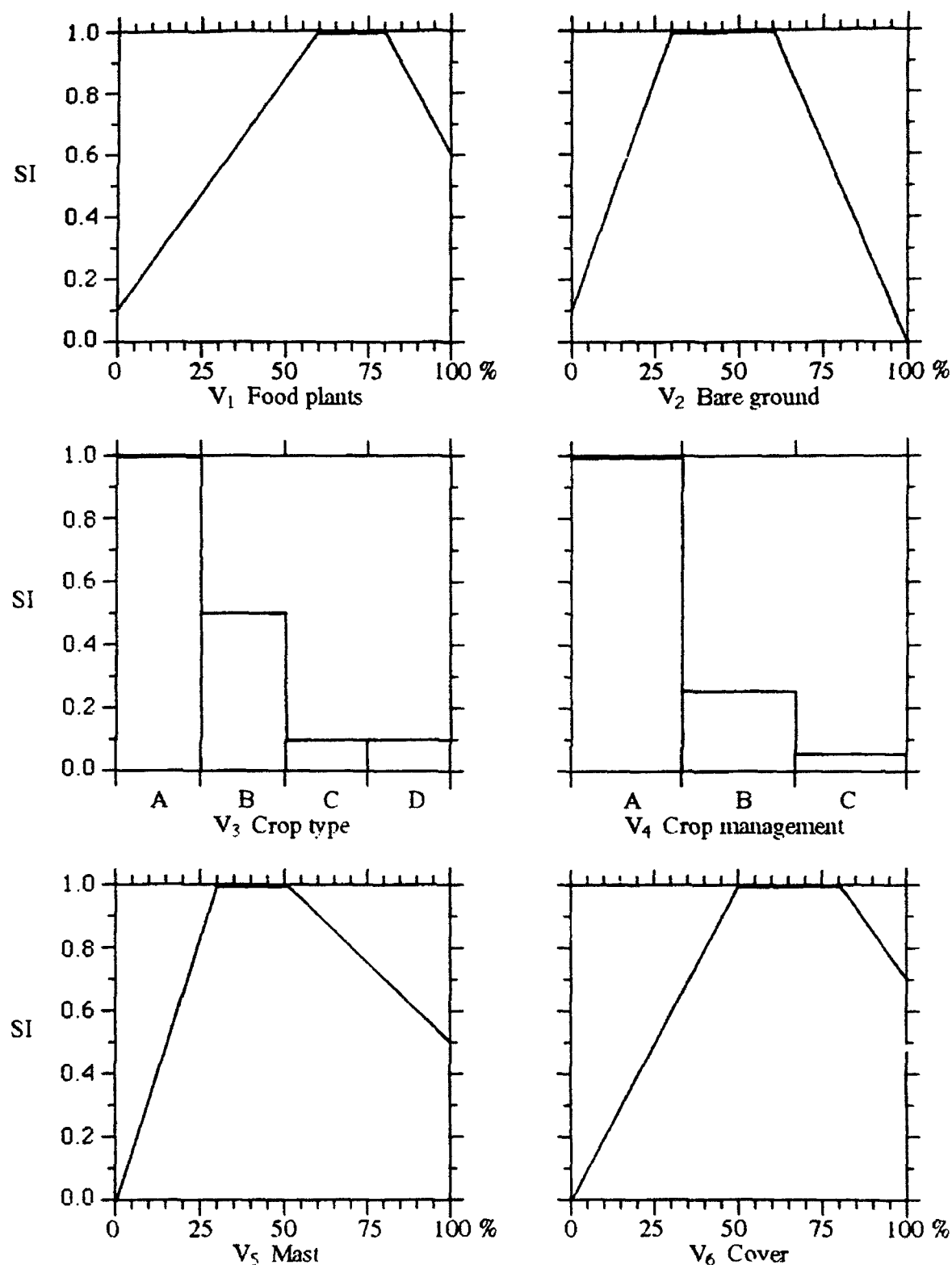
Fig. 2 Variables from the draft bobwhite HSI model (Schroeder 1983).
Crop Type: A - corn, soybeans, cowpeas, or peanuts. B - other grain
crops. C - vegetable or fruit crops. D - fiber crops and tobacco.
Crop Management: A - majority of residues remain. B - majority of
residues removed, land not plowed. C - residues plowed under.

(Sheet 1 of 3)
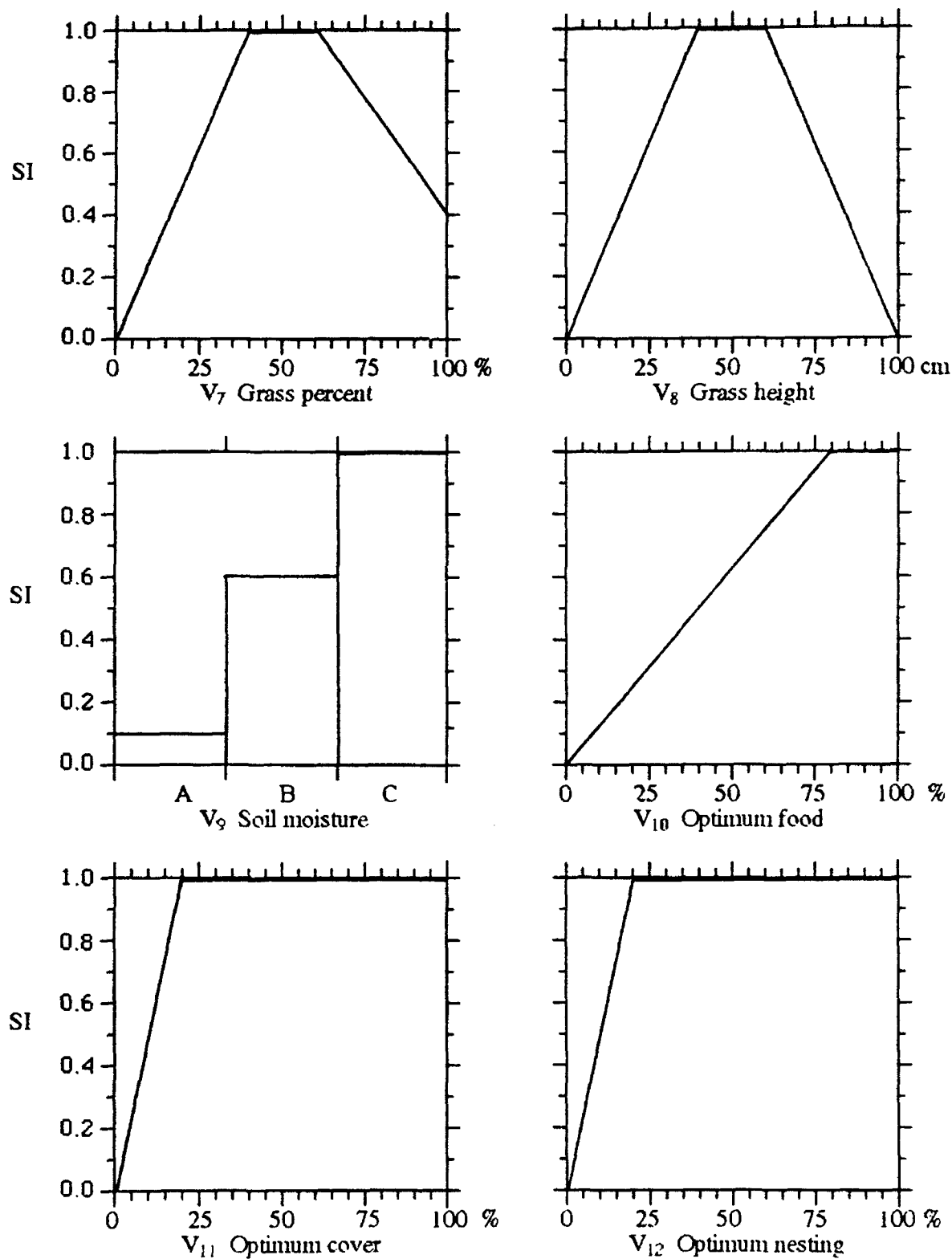
Fig. 2. Extended. Soil Moisture: A = typically moist to saturated.
B = moderately dry to moist. C = typically dry. (Sheet 2 of 3)
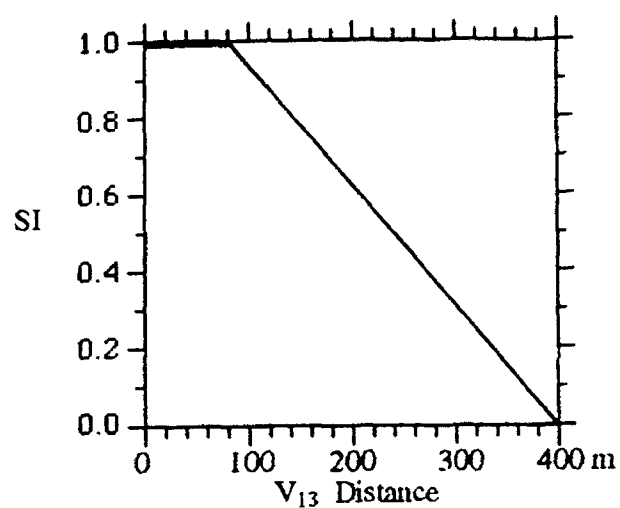
Life requisite	Cover types	Equation
Winter food	DF	$\dfrac{3(V_1 \times V_2)^{0.5} + 2V_5}{4}$
	DS, G, F, PH	$\dfrac{3(V_1 \times V_2)^{0.5}}{4}$
	C	$\dfrac{(3V_1 + V_3) \times V_4}{4}$
Cover	DF, DS	V_6
Nesting	G, F, PH	$(V_2 \times V_7 \times V_8)^{0.5} \times V_9$

Fig. 2. Extended. Cover type names were defined in Table 2.

(Sheet 3 of 3)

Data Collection

Quail censuses on 7 of the 9 study sites were conducted by
researchers from UT. The other 2 sites were censused by personnel from
WES under direction of a UT researcher to assure data compatibility.
Censuses were conducted on 5-9 December 1982. The technique used was a
walk census by 5 people walking abreast in sequential sweeps over a
study area and counting the number of coveys and covey members. The
location of birds that landed was noted to avoid double counting. UT
researchers used the same technique to census 8 of the 9 areas in
December 1983.

Prior to field work, vegetation cover types were delineated using
black and white aerial photographs taken in September 1982 at a scale of
1:7,290. Designation of cover types followed the guidelines for HSI
models (U.S. Fish and Wildlife Service 1981). The hectares in each
cover type on each site were determined by drawing their boundaries on
mylar and using a planimeter. Types identified were forest (DF),
shrubland (DS), forbland (F), grassland (G), pasture/hayland (PH), and
cropland (C). The shrub, savanna, and forest cover types were further
determined to be deciduous or evergreen. Evergreen vegetation was
uncommon on the study areas and was subsequently included with deciduous
types.

A pilot study was conducted 28-30 July 1983 to determine sampling
techniques and verify cover types. Data to run the model were collected
on 12-30 September 1983 by a 4-person team from WES.

The number of sampling locations in each study area was determined
using a stratified random design based on the extent of each cover type.

Between 8 and 20 locations were selected (Table 4). At each location, 1-3 randomly placed transects were established and data collected on the transect or on lines extending to either side. This resulted in 40-83.:% of each area being sampled (Table 4). Details of the sampling plan varied with the cover type and variable as illustrated in Fig. 3.

At 10-m intervals on the 100-m transect in forest and savanna, 5-m lines were extended to alternate sides and the variables of Food Plants, Bare Ground, Grass Percent, and Grass Height were measured by point sampling at 5 points on each line. The variable of Mast was measured at 20 points along the transect using an optical tube for a reading of presence or absence of overhead foliage. Cover was estimated at 10 m^2 plots on the transect.

The same design was followed in shrubland vegetation for Food Plants, Bare Ground, and Cover, except that lines were run at 5-m intervals from a 50-m transect. In the non-woody cover types, measurements were taken on a 25-m transect with 25 points instead of 50.

Crop Type and Crop Management were based on visual examination of agricultural fields. Soil Moisture was based on visual evidence of moisture.

Data Tabulation

Because sampling for model variables was conducted in the fall of 1983, use of census data from December 1983 was more appropriate than data from 1982. The Demo Farm was not censused in 1983, but 1982 data were used in analysis because no land use changes occurred over the year and no or very little variation in bobwhite numbers was expected for that site.

Table 4. Number of sample sites, percent of area sampled, and hectares sampled, by study area and cover type on the Ames Plantation, Grand Junction, Tennessee.

Study area	No. of sample sites	% of area sampled	Deciduous forest (DF)		Tree savanna (TS)		Deciduous shrub (DS)		Forbland (F)		Grassland (G)		Pasture/ hayland (PH)		Cropland (C)	
BC	15	62.2	4	11.70			3	1.38	3	1.90	1	2.87	0		4	16.63
DM	8	83.5	2	16.79			2	0.20	1	0.20	0		3	44.31	0	
ES	18	72.2	6	31.65			3	0.73	3	1.58	2	1.90	0		4	12.67
HP	20	70.8	5	51.32			3	0.93	3	8.62	4	6.68	2	5.14	3	21.12
MM	16	66.0	5	49.25			3	1.50	2	1.25	2	2.14	0		4	9.55
RS	11	40.0	5	11.82			1	0.32	2	1.17	3	0.57	0		0	
TE	16	56.8	2	3.08			6	7.53	3	6.64	1	0.04	0		4	14.65
TW	11	72.6	3	14.49	3	20.40	2	0.10	2	5.67	0		0		1	0.16
WP	11	62.6	6	22.02			1	0.69	1	1.29	1	0.57	1	2.67	1	11.86
Total	126		38	212.12	3	20.40	24	13.38	20	28.32	14	14.77	6	52.12	21	86.64

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Forest (100 m)

V1   Food plants   •
V2   Bare ground   •
V5   Mast   □
V6   Cover   ▮ ▮
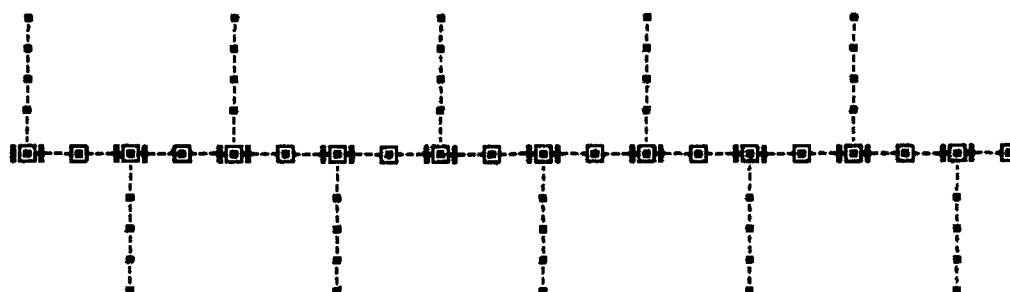
Shrubland (50 m)

V1   Food plants   ▪
V2   Bare ground   ▪
V6   Cover   ▮ ▮
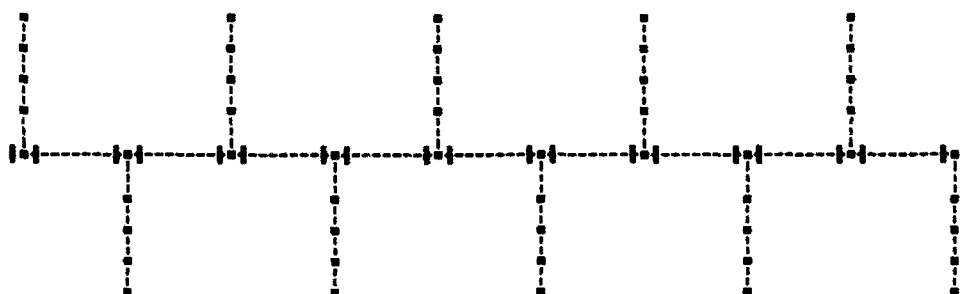
Forbland, Pasture/Hayland, Grassland (25 m)

V1   Food plants   ▪
V2   Bare ground   ▪
V7   Grass percent ▪
V8   Grass height ▪
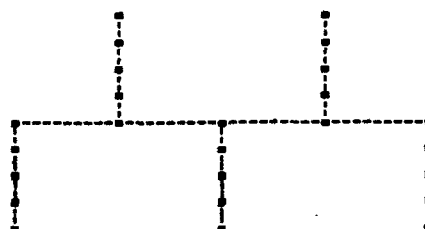
Fig. 3. Illustration of sampling plan used in test of the draft
bobwhite HSI model (Schroeder 1983) on the Ames Plantation, Grand
Junction, Tennessee, by cover type and variable, for continuous
variables. Diagram not to scale.

Quail numbers were expressed as number of coveys and total number of birds on an absolute basis, and converted to a per hectare basis because the study areas were different sizes. In addition, for ease in interpreting some tests, it would be desirable to show density on the same 0 to 1.0 basis as SI and HSI scores. Therefore, each density expression also was indexed to 1.0. Several additional ways to portray density were calculated to allow consideration of other measures for use as the standard of comparison for model modification. Data from 1982 were treated the same way to provide a comparison between years.

Measurements from each line and transect were combined to obtain a value for each model variable on a sampling location, then values from these locations were treated in 1 of 3 ways. Measurements for Crop Type, Crop Management, Cover, and Soil Moisture were converted directly to SI scores because they were category data.

All continuous variables received 2 treatments. The first was to average measurements from each sampling location within a cover type. The second was to use a weighted average based on the number of hectares in the location. Each variable value was multiplied by the hectares in the sampling location, summed within a cover type, then divided by the total hectares in that cover type.

The variable of distance was calculated from measurements on the cover type maps. Values for Optimum Food, Cover, and Nesting were calculated by Micro-HSI version 2.1 software supplied by the FWS, which also was used to determine SI and HSI values. The software was modified by Mr. Warren Mangus to allow one-time input of interspersion values.

The HSI was calculated as follows (Fig. 4). The SI for each of the

Cover
Type

DF
V(Food plants) → SI
V(Bare ground) → SI ⟶ Food LRSI * UA[a] = AMSI
V(Mast) → SI

DS,
F,G,
PH
V(Food plants) → SI
V(Bare ground) → SI ⟶ Food LRSI * UA = AMSI[b]

C
V(Food plants) → SI
V(Crop type) → SI ⟶ Food LRSI * UA = AMSI
V(Crop management) → SI

Σ ⟶ Food EOA ⟶ FSI

F, G,
PH
V(Bare ground) → SI
V(Grass percent) → SI
V(Grass height) → SI ⟶ Nesting LRSI * UA = AMSI[b] ⟶ Nesting EOA ⟶ NSI
V(Soil moisture) → SI

DF,
DS
V(Cover) → SI ⟶ Cover LRSI * UA = AMSI[b] ⟶ Cover EOA ⟶ CSI

minimum ⟶ HSI

[a] UA = relative area * AII
[b] AMSIs are summed by cover type

Fig. 4. Process of calculating HSI scores from variables measured in the field in the draft bobwhite HSI model (Schroeder 1983).

first 9 variables (V) was calculated in each cover type from its curve
(Fig. 2). Within each of the 3 Life Requisites (LR), equations were
used to combine the SIs into a Life Requisite Suitability Index (LRSI)
for each cover type. For a cover type that supplied the LR, the LRSIs
were multiplied by the relative area (the percent of the entire study
area) in that cover type. If a cover type could not supply the LR, its
LRSI - 0. The lack of a LR in a cover type reduced the value of the
other LRs that it did supply, i.e., the area was not self-contained
habitat for the bobwhite. The reduction in value was a function of the
degree of interspersion with other cover types that could provide the
missing LR.

The degree of interspersion was determined with an Average
Interspersion Index (AII). I placed a 20-dot grid in a random position
over the cover type map and when a dot fell in a cover type missing a
LR, measured the distance to the nearest cover type that could supply
it. Between 3 and 20 points were used, depending on the extent of the
cover type. The SI for each of those distances was obtained and the
mean value applied to the curve for V13, Distance, (see Fig. 2), to
determine the AII.

The AII was multiplied by the relative area of the cover type to
derive Usable Area (UA). When the AII was optimum (1.0), relative area
and UA were equivalent. The LRSI was then multiplied by the UA,
resulting in an Area-Modified SI (AMSI). AMSIs were summed over all
cover types, and the 3 sums (1 for each LR) were the Equivalent Optimum
Areas (EOA) for the LRs. The EOAs were read on the X axis of the curves
for Optimum Food, Optimum Nesting, and Optimum Cover, producing the SI

for each LR in the study area. The lowest of these 3 values (FSI, NSI, or CSI) became the HSI.

Selected spatial measurements were derived to provide potential alternate model variables. Based on the premise that bobwhite require high interspersion and juxtaposition of suitable areas that provide their needs, spatial patterns related to cover types were examined. Items were each cover type unit's size (mean, median, maximum, and minimum), the number of units per site and per hectare, the percent composition of that unit in the site, and summary measures such as the grand mean. Fried's Index (Fried 1975) was calculated and examined along with spatial characteristics of the entire study site such as the ratio of perimeter to hectare.

Data Analysis

Characteristics of the model variable data were determined through correlation and distribution analyses using Microstat 4.1 (Ecosoft, Inc., Indianapolis, IN). Variables were examined for their behavior within cover types, within study areas, and in comparison to each other. The same analysis was performed on the data sets of SI and LRSI values.

To find areas of the model's performance that could be improved, correlation analysis was performed on bird density and the values of the variables, the SI for each of those variables, the LRSIs and AMSIs, total EOA for each LR (winter food, nesting, cover), and their resulting SIs. The category variables were excluded from some analyses because they showed insufficient change among sites. Scatterplots were run on correlations that were significant at $P \geq 0.10$ and that were not spurious or nonsensical. Correlations were considered spurious if the 2

factors being correlated had a common basis of derivation (Kenney 1982) and nonsensical if there was no possible logical meaning to the relationship. Plots were examined for patterns and trends. Tables in Lewis (1984) were used to determine significance levels.

Modification of the model followed. Changes suggested by the data or literature were implemented and evaluated independently, then in combination with each other. When maximum improvement in performance at 1 level of the model was accomplished, the next level was examined. Modifications attempted included deleting variables, changing SI curves, and changing the mathematical relationships. Spatial measures were analyzed for their relationship to census results.

RESULTS

Quail Populations and Standard of Comparison

Censuses on the 9 study areas in 1983 produced quail numbers between 0 and 3.28 birds/ha (Table 5) with an average of 1.0 bird/ha. Area BC had the highest population in both the number of birds and coveys, even though it was the second smallest area. There were 5 coveys per study area on the average, with 12 birds/covey.

In 1982, BC had the second highest number of birds while HP and MM had no quail (Table 6). Conditions on RS were adequate for quail, in contrast to 1983. There were 4 coveys per study area on the average, with 13 birds/covey.

Normality of distribution varied among the expressions of density. The 2 covey/ha variables failed the normal curve goodness of fit test at $P < 0.5$, and the 4 variables for number of birds and birds/ha failed at $P = 0.08$. Therefore, both parametric and non-parametric tests were run.

Excluding values of 1.0, the mean Pearson correlation among 40 expressions of quail density in 1983 was 0.881 and the mean Spearman correlation was 0.922. (All $n = 9$ and $P < 0.001$ unless otherwise indicated). Excluding analyses involving birds/covey and values of 1.0, Pearson correlations between 24 expressions of bird density ranged from $r = 0.907 - 0.991$ and averaged 0.964. The relationship between 16 expressions of the number of birds/covey and other density expressions gave r values of 0.741 - 0.776 ($P < 0.02$). Spearman correlation gave similar results for the first 24 relationships (range of $r = 0.895 - 0.996$, $P < 0.01$) and averaged 0.949. The 16 values for birds/covey were higher at 0.765 - 0.933 ($P < 0.05$) and averaged 0.879.

Table 5. Alternate expressions of bird density from censuses conducted in December 1983 on the Ames Plantation, Grand Junction, Tennessee.

Study area	No. of coveys	No. of coveys indexed	Coveys /ha	Coveys /ha indexed	No. of birds	No. of birds indexed	Birds/ covey	Birds/ covey indexed	Birds /ha	Birds/ha indexed
BC	12	1.00	0.22	1.00	182	1.00	15.17	0.99	3.28	1.00
DM	2*	0.17	0.03	0.14	19	0.10	9.50	0.62	0.26	0.08
ES	6	0.50	0.09	0.41	81	0.45	13.50	0.88	1.21	0.37
HP	3	0.25	0.02	0.09	33	0.18	11.00	0.72	0.25	0.08
MM	8	0.67	0.08	0.36	69	0.38	8.62	0.56	0.71	0.22
RS	0	0	0	0	0	0	0	0	0	0
TE	6	0.50	0.11	0.50	83	0.46	13.83	0.90	1.48	0.45
TW	8	0.67	0.14	1.64	123	0.68	15.37	1.00	2.19	0.67
WP	1	0.08	0.02	0.09	8	0.04	8.00	0.52	0.13	0.04

* 1982 Data

Table 6. Alternate expressions of bird density from censuses conducted in December 1982 on the Ames Plantation, Grand Junction, Tennessee.

Study area	No. of coveys	No. of coveys indexed	Coveys /ha	Coveys /ha indexed	No. of birds	No. of birds indexed	Birds/ covey	Birds/ covey indexed	Birds /ha	Birds/ha indexed
BC	7	0.78	0.13	1.00	101	0.86	14.43	0.92	1.82	1.00
DM	2	0.22	0.03	0.23	19	0.16	9.50	0.61	0.26	0.08
ES	9	1.00	0.13	1.00	118	1.00	13.11	0.84	1.76	0.97
HP	0	0	0	0	0	0	0	0	0	0
MM	0	0	0	0	0	0	0	0	0	0
RS	3	0.33	0.09	0.69	47	0.40	15.67	1.00	1.36	0.75
TE	5	0.56	0.09	0.69	72	0.61	14.40	0.92	1.28	0.70
TW	6	0.67	0.11	0.85	86	0.31	14.33	0.92	1.53	0.84
WP	2	0.22	0.03	0.23	17	0.14	8.50	0.54	0.27	0.15

Similar strong relationships were present in the 1982 quail numbers. Mean Pearson and Spearman correlations for all relationships excluding values of 1.0 were 0.900 and 0.881, respectively. Those excluding birds/covey were 0.949 and 0.965, while the subset involving birds/covey were correlated with means of 0.820 and 0.749.

While some of these relationships were spurious (Kenney 1982), their strength and the linearity of their scatterplots allowed selection of 2 density measures to serve in lieu of the others. The 2 most useful expressions for use as a standard of comparison were indexed coveys/hectare and indexed number of birds/hectare. 1983 data showed Spearman correlations between them of $r = 0.987$, slope 0.987, and intercept 0.063, indicating that either could be used. In the 1982 density data, those values were 0.987, 0.975, and 0.126, respectively.

There were 2 exceptions to the linear nature of the scatterplots of 1983 data. One was study area MM in those expressions that included number of coveys, because of its large number of coveys but small covey size. The second involved variables for birds/covey, which had less predictive value (high intercepts, low slopes, and greater scatter).

Data for the model variables collected in the fall of 1983 were more closely related to the upcoming winter conditions and 1983 censuses than the 1982 censuses. From this and the above information, I decided to use indexed birds/hectare from 1983 as the standard of comparison; it is hereafter referred to as density.

Initial Model Scores

Initial HSI scores were between 0.19 and 1.0 (Table 7) and averaged 0.50. The limiting LRs were winter food on 3 areas (DM, HP, and TE) and

Table 7.   HSI and LRSI scores and EOA sums for 9 study areas on the Ames Plantation, Grand Junction, Tennessee, based on data from 1983 and the draft model (Schroeder 1983).

Study area	HSI	Food EOA	FSI	Nesting EOA	NSI	Cover EOA	CSI	Density
BC	0.52	77.25	0.97	10.42	0.52	16.59	0.83	1.00
DM	0.49	39.53	0.49	32.35	1.00	11.20	0.56	0.08
ES	0.52	74.85	0.94	10.49	0.52	20.69	1.00	0.37
HP	0.48	38.24	0.48	15.40	0.77	27.09	1.00	0.08
MM	0.19	24.42	0.31	3.78	0.19	23.21	1.00	0.22
RS	0.27	33.57	0.42	5.38	0.27	18.76	0.94	0
TE	0.81	64.68	0.81	20.16	1.00	27.26	1.00	0.45
TW	1.00	84.77	1.00	54.01	1.00	25.27	1.00	0.67
WP	0.22	32.75	0.41	4.36	0.22	21.88	1.00	0.04

nesting on the other 5. Cover was never limiting. Interspersion was optimum or high on all but area MM, which registered interspersion for nesting of 0.54 in type DF and 0.79 in type C. Interspersion on the other 50 combinations of cover types and LRs was 1.0 in 28 and an average of 0.96 in 22, with the minimum value 0.88.

Nesting:--To illustrate the calculations of the model, derivation of the lowest score is explained here. Area MM had an HSI of 0.19 because the NSI was 0.19. Nesting was a function of 4 variables (Bare Ground, Grass Percent, Grass Height, and Soil Moisture) measured separately in cover types F, G, and PH. In cover type F on MM, the amount of Bare Ground (75%) was too high and Grass Height too great (80 cm) so the resulting SI was 0.52. In cover type G, the amount of Bare Ground was too high (70%) and Grass Cover was too dense (81%); that SI was 0.72. There was no cover type PH on area MM. The model assumed that no suitable nesting habitat occurred in cover types DF, DS, and C so their nesting LRSI was 0.0. In type F and type G, the LRSIs of nesting (0.52 and 0.72) multiplied by UAs of 2.3 and 3.6 ha in type F and type G, respectively (AII - 1.0 in both cases), then summed, gave a nesting EOA of 3.78%. This produced an overall nesting value of 0.19 (see Fig. 2 V12).

On study area BC, nesting quality led to an HSI of 0.52 because of less than optimum conditions overall in type F (LRSI of 0.63). In type G, Soil Moisture and too dense a Grass Cover lowered that LRSI to 0.51. The larger UA of type F (12.4 ha) dominated the UA of 5.2 ha for type G and its LRSI of 0.51; the EOA was 10.4% and the NSI and HSI 0.52.

Nesting conditions in cover type G on area ES rated a 0.33 because of

only 3.5% Bare Ground and too dense and tall a Grass Cover. But the UA of type G (2.8 ha) was less than the 9.8 ha of type F (LRSI 0.97), which gave an EOA of 10.5% and an HSI of 0.52.

Study area RS was 54% type PH in dense herbaceous cover with nearly no grass and an LRSI of 0.005. Cover types F and G had Grass Cover too thick and tall, producing LRSIs of 0.47 and 0.50. The PH type contributed an EOA of only 0.26%, so the total nesting EOA was 5.38% for the third lowest HSI of 0.27.

Nesting scores on WP were low because of too dense and too low Grass Cover in type PH, too sparse and too low Grass Height in type F, and too dense Grass Cover with too little Bare Ground in type G. These types also were small in UA which combined to produce an EOA of 4.36% and the second lowest HSI of 0.22.

Although not limiting, scores for nesting less than 1.0 also were obtained on HP. Limits on nesting were from too little Grass Cover and too much Bare Ground.

Winter food:--All cover types have an assumed capability to produce winter food. In cover types other than C and DF, a suitable percentage of Food Plants ccmbined with adequate Bare Ground provides feeding habitat. Crop Type, Crop Management, and Food Plants were evaluated in cultivated areas. In cover type DF, the variables for herbaceous types were combined with the percent cover of woody plants that produce Mast. Any cover type that did not produce food could still be assigned some value for the other LRs if interspersion was adequate. The EOA for each cover type was derived as for nesting.

Winter food was limiting on DM because of a lack of Food Plants in

all cover types but type F, which had 36%, and a small UA (2.7 ha).
Type PH contributed most of the EOA for winter food because of a large
UA (63.4 ha) even though there was only 7% cover of Food Plants.

Food quality in HP also was low because of extremely low percentages
of Food Plants. Most of the food value came from Mast production in the
type DF which occupied a UA of 28.1 ha.

Study area TE was kept from an optimum score by low values for Food
Plants in type DS, which occupied a UA of 30.9 ha but scored an LRSI of
only 0.24. The amount of both Bare Ground and of Food Plants was 10%.

Scores less than 1.0 were also obtained on MM, RS, and WP for winter
food. These areas had poor Crop Management practices and too low a
value for Food Plants.

Cover:--Although cover was never limiting, it scored less than
optimum on areas BC (0.83), DM (0.56), and RS (0.94). In all 3 cases,
this was due to SI values for Cover of approximately 0.5 in type DF,
with large UAs of 23-34 ha. Cover was produced in type DS where SI
values also were low, but the UA was small so the effect was negligible.

Condition of the Variables and SIs

Comparison of the values obtained for each variable using weighted
and non-weighted averaging, either across cover types or within cover
types, showed differences too small to affect the SI calculations. The
mean difference was 0.77%, the largest difference was 3.60%. I used
weighted averaging because it effectively increased the area sampled
under an assumption of homogeneity within a sample unit.

Independence among variables was examined by correlation analysis.
Across all study areas and within cover types, significant relationships

were found between Bare Ground and Cover, Grass Percent, and Soil
Moisture in 4 cover types (Table 8). Grass Percent and Soil Moisture
were correlated in type F. A positive relationship existed between Food
Plants and Bare Ground and between Food Plants and Grass Height in
multiple cover types. I found the positive correlations either too low
or too irregular to be meaningful and therefore obstructive in analysis.
The negative correlations appeared important to the life requirements of
the quail. Therefore, none of the interrelated variables were removed
from analysis.

To determine if an adequate range of conditions had been sampled,
actual distribution of each variable was compared to potential
distribution as portrayed in the model (Fig. 5). Mast, Optimum Cover,
and Optimum Distance variables covered $\leq$ 50% of the entire range of
potential values. Category data were more limited. The distribution of
all variables was skewed as shown by the median values, with Mast, Grass
Height, and Optimum Cover the least skewed.

Distributions of individual variables within cover types were
examined more closely because of their potential effect on the
interpretation of analysis. Values for Food Plants, Bare Ground, and
Grass Height were very low in some cover types which had the effect of
clustering points and reducing ability to distinguish among areas and
habitat conditions. Food Plant occurrence was especially low in type DF
(0-23%, median 2%), type DS (0-10%, median 4%), and type PH (0-7%,
median 1%), and slightly higher in type G (0-38%, median 27%) and type C
(0-49%, median 12%). Values for Bare Ground in type DF were 5-30% and
in type DS 1-19%, with medians of 20% and 9%, respectively. The range

Table 8. Significant Pearson correlations among variables in the draft bobwhite HSI model (Schroeder 1983) tested on the Ames Plantation, Grand Junction, Tennessee.

Cover type	Variables	Sample size	Correlation
DF	Bare ground, cover	9	-0.718^b
DS	Bare ground, cover	9	-0.828^c
F	Bare ground, grass percent	9	-0.650^a
	Bare ground, soil moisture	9	0.744^b
	Grass percent, soil moisture	9	-0.658^a
G	Bare ground, grass percent	7	-0.746^b
F, G	Bare ground, grass percent	16	-0.654^c
DF, DS	Bare ground, cover	18	-0.773^c
DF, DS, F, G	Food plants, bare ground	34	0.498^c
F, G, PH	Food plants, grass height	20	0.423^a
DF, DS, F, G, PH	Food plants, bare ground	38	0.389^b

[a] $P < 0.10$
[b] $P < 0.05$
[c] $P < 0.01$

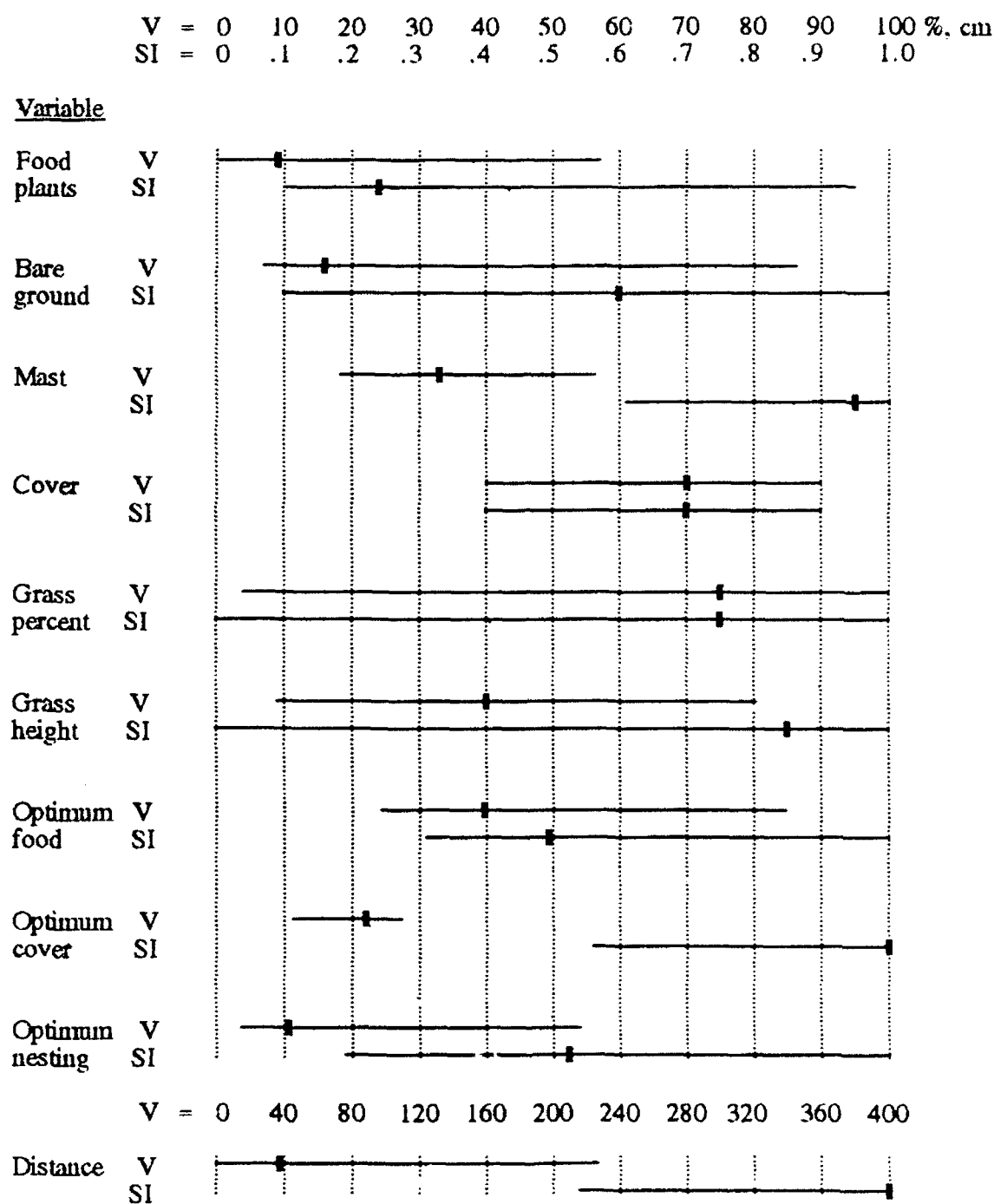Fig. 5. Range (horizontal line) and median value (block) of variables and their SIs over all cover types on the Ames Plantation, Grand Junction, Tennessee. All variables except Grass Height and Distance have a potential value of 0-100%. Grass Height has a potential value of 0-100 cm and Distance of 0-400 m. Median values for Crop Type, Crop Management, and Soil Moisture were 1.0, 1.0, and 0.97, respectively.

of values for Grass Height in type PH was 1-15% with a median of 8%.

Values were clustered on the high end for Cover in type DS (0.7-0.9, median 0.7), Grass Percent in type G (41-100%, median 87%), and Soil Moisture in all types (0.6-1.0, median 1.0). In type C, all values of Crop Type were optimum; for Crop Management, 5 of 7 areas with that cover type were optimum. Values were centered in type DF for Cover (0.4-0.7, median 5) and in type G for Grass Height (31-67 cm, median 60 cm).

Of the calculated variables, Optimum Food was the highest with EOA at 24-85%, median 40%. Values were low in Optimum Cover (11-27%, median 22%) and Optimum Nesting (4-54%, median 11%).

The distributions of the SIs also were examined because of their potential effect on the interpretation of correlations and because modification of the SI curve was a possible step in improving the model's performance. Ideally, study areas should have variables with a range of SIs from 0-1.0 and with data points on ascending, level, and descending parts of the curves. Several variables did not exhibit this pattern (Fig. 5).

The SI for Food Plants matched the variable in having a very narrow distribution, especially in type DS and type PH; there were no values in any cover type in the descending portion of the SI curve. SI scores for Bare Ground were clustered low in type DS but high in type F where 5 of the 9 study areas scored 1.0. The SI was always 1.0 for Crop Type, and either 0.1 or 1.0 for Crop Management. All SIs for Mast were $\geq$ 0.94 except area BC with a score of 0.61. Most of the values for Grass Percent were on the descending slope of the SI curve. Grass Height was

low in type PH and high in types F and G.

In the calculated variables, the lowest SI for Optimum Cover (CSI) was 0.56 and its median value was 1.0. The SI for Optimum Food (FSI) was 0.31 - 1.0 and for Optimum Nesting (NSI) 0.19 - 1.0. Both median values were 0.5.

Relationship Between Bobwhite Populations and Initial Model

HSI scores were normally distributed, but indexed birds/hectare (density) failed normality at $P = 0.8$. Therefore, both parametric and non-parametric analyses were run when appropriate. Density was correlated with HSI scores (Pearson $r = 0.582$, $n = 9$, $P < 0.10$; Spearman $r = 0.711$, $P < 0.05$). A scatterplot of the Pearson analysis (Fig. 6) had an intercept of 0.351 and slope of 0.463. Areas DM, HP, TE, and TW were above the regression line; ES was on the line; and the others below. The scatterplot for the Spearman analysis had an intercept of 1.429 and a slope of 0.714. Only areas BC and WP were below the regression line.

The unsatisfactorily low correlation between density and HSI led to 2 investigations. One was to determine why the model generally produced higher scores than bird numbers, which included determining what factors had the most effect on the HSI. The second was to find the reason for the low HSI score of BC compared to both density and the other study areas. This order of investigation was set because of the possibility of BC being an irregular site, while nearly all the other sites received elevated scores.

Role of All LRSIs:--From comparisons of HSI values against the FSI, NSI, and CSI values, it appeared that food was responsible for the
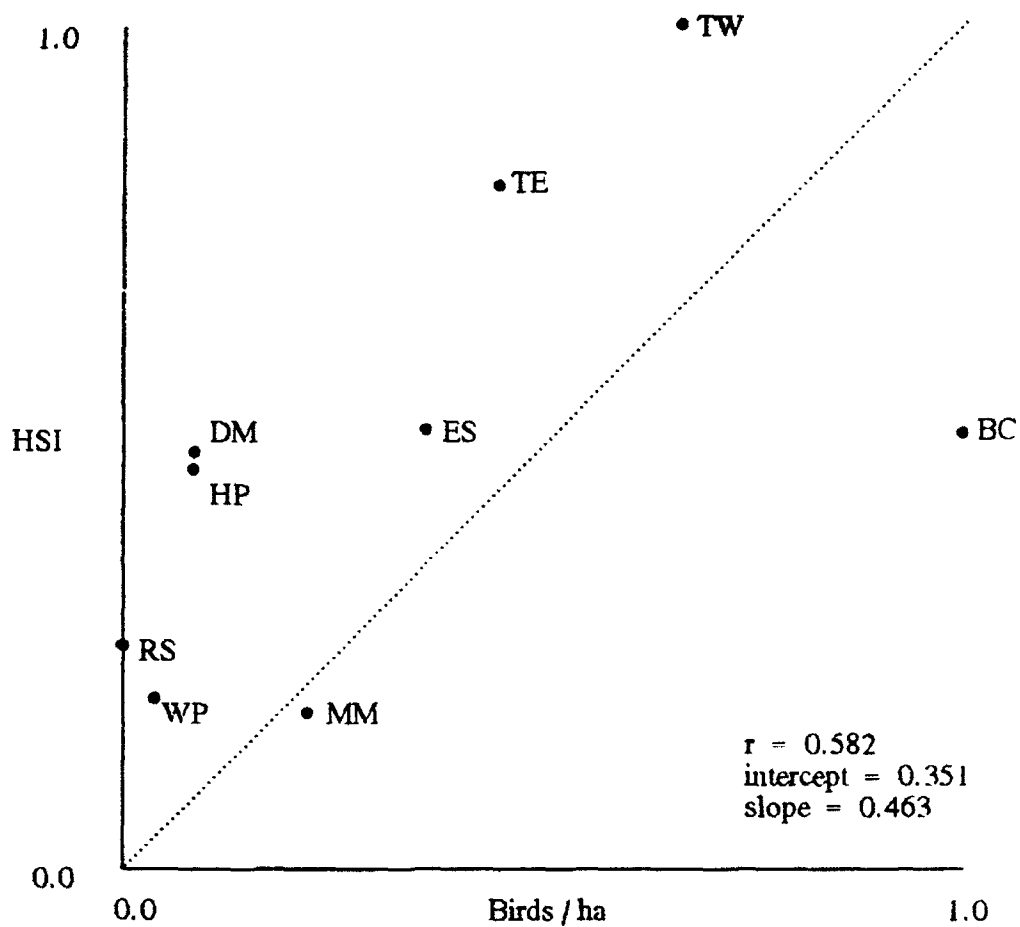
Fig. 6. Scatterplot of HSI scores and birds/hectare on each study area on the Ames Plantation, Grand Junction, Tennessee, from the draft model (Schroeder 1983) with no modifications. Study area names were defined in Table 2.

elevated scoring pattern. With the exception of BC and MM, the model rated habitat quality on the study areas higher than indicated by quail density and FSI scores were even higher (Table 7). Five of the 9 study areas rated higher in FSI than HSI. FSIs plotted against HSIs verified that winter food was responsible for the elevated scores, with a Pearson r = 0.792 (n = 9, P < 0.01), an intercept of 0.238, and a slope of 0.816. Sites BC and ES were above the regression line. A scatterplot and correlation analysis of HSI against CSI gave no useful information or pattern (r = 0.042). Because NSI = HSI on 5 of the areas, that relationship was strong (r = 0.848, n = 9, P < 0.01), intercept 0.067, and slope 1.086.

FSI and density were correlated (Pearson r = 0.839, n = 9, P < 0.01), and a scatterplot showed an intercept of 0.424 and slope of 0.689. Spearman correlation was 0.778 with an intercept of 1.092 and slope of 0.782. FSI scores were higher than density by an average of 0.34 (Table 7). Neither Pearson or Spearman correlation of CSI and NSI with density gave useful or significant results (r = < 0.385).

One step back from calculation of the FSI, NSI, and CSI is the EOA for food, nesting, or cover summed for all cover types in a study area. When analyzed with quail density, correlation values, slopes, and intercepts similar to FSI, NSI, and CSI were found (r = 0.836 for food with high intercept and low slope, no significant relationship for nesting or cover).

Role of Food:--Food scores at the next level of calculation are a function of 3 items: the interspersion between cover types that can and those that cannot provide food, the presence and extent of cover types

that can provide food, and the percent cover and condition of food plants in those cover types. Because all cover types could and did provide food scores > 0, interspersion did not become a factor.

Because a cover type with larger area and low food score contributes more to the EOA than a small area with a higher score, I examined the relative role of variables and area in determining food EOA (Table 9). Cover type DF was the most influential in determining EOA scores because of its presence at all sites, its large UA, and relatively high food score (average of 0.68). It was the largest contributor for sites ES, HP, MM, RS, and WP; and the second largest for sites BC, DM, and TW. Sites BC and TE were most influenced by type C, which was the primary weight in site BC and co-equal with DF in site ES. Site DM received most of its food EOA from type PH, and TW from the savannah cover type.

The apparent importance of food in type DF was explored by comparing density with the SI for total food value in DF, the SI for each of 3 variables, and the measures of the variables themselves. The clear relationship between density and model components deteriorated somewhat at this point (Table 10). However, Food Plants in types DF and F showed a positive linear relationship and Bare Ground in type F a negative trend. The other food variable/cover type combinations had no discernible pattern; there was often high scatter in the scatterplots, too narrow a range of values to provide any explanations, or outliers that falsely increased the correlation coefficient. Too little variation existed for the variables of Crop Type and Crop Management for analysis. No non-linear relationships were found when I looked at squared and cubed values.

Table 9. Relative contribution to food EOA in each cover type from LRSI equations versus Usable Area on the Ames Plantation, Grand Junction, Tennessee.

Study area	DF			DS			F			G			PH			C		
	LRSI	UA	Food EOA	Food LRSI	UA	Food EOA	Food LRSI	UA	Food EOA	Food LRSI	UA	Food EOA	Food LRSI	UA	Food EOA	Food LRSI	UA	Food EOA
BC	0.65	25.3	16.5	0.20	4.8	0.9	0.53	12.4	6.6	0.39	5.2	2.0	0	0	0	1.00	51.1	51.1
DM	0.70	23.4	16.3	0.14	0.8	0.1	0.60	2.7	1.6	0	0	0	0.34	63.4	21.5	0	0	0
ES	0.72	48.1	34.4	0.15	2.9	0.5	0.69	9.8	6.7	0.26	2.8	0.7	0	0	0	1.00	32.5	32.5
HP	0.65	39.2	25.4	0.17	2.4	0.4	0.40	12.4	4.9	0.37	5.3	2.0	0.16	7.4	1.2	0.16	27.0	4.4
MM	0.60	29.9	18.0	0.10	2.5	0.3	0.46	2.3	1.1	0.50	3.6	1.8	0	0	0	0.12	28.5	3.3
RS	0.72	34.0	24.4	0.27	1.5	0.4	0.43	7.1	3.0	0.38	3.4	1.3	0.08	53.7	4.5	0	0	0
TE[a]	0.74	9.1	6.7	0.24	30.9	7.4	0.68	19.9	13.5	0.22	2.4	0.5	0	0	0	1.00	36.6	36.6
TW	0.72	25.2	18.1	0.29	0.6	0.2	0.73	19.1	14.0	0	0	0	0	0	0	1.00	16.2	16.2
WP	0.65	35.0	22.8	0.13	2.2	0.3	0.56	5.4	3.1	0.36	1.7	0.6	0.19	4.3	0.8	0.11	48.4	5.2
Mean	0.68	29.9	20.3	0.19	5.4	1.1	0.56	10.1	6.1	0.35	3.5	1.3	0.19	32.2	0.7	0.63	34.3	21.3

[a] Area TW also had a Food EOA of 36.3 from LRSI = 1.0 and UA = 36.3 ha in Tree Savanna.

Table 10. Spearman correlations of density and FSIs, SIs, and variables for food by cover type at the Ames Plantation, Grand Junction, Tennessee.

Cover type	Sample size	r for FSI	Variable	r for SI	r for variable
DF	9	0.319	Food plants	0.691[a]	0.686[a]
			Bare ground	0.113	0.151
			Mast	-0.558	0.160
DS	9	0.318	Food plants	-0.008	-0.008
			Bare ground	0.378	0.378
F	9	0.527	Food plants	0.703[a]	0.703[a]
			Bare ground	0.092	-0.126
G	7	0.118	Food plants	-0.601	-0.601
			Bare ground	0.614	0.205
C	7	0.875[b]	Food plants	0.171	0.171
PH	4	0.632	Food plants	0.889	0.738
			Bare ground	0.632	0.949

[a] significant at < 0.05
[b] significant at < 0.01

To derive the food LRSI in type DF, SIs for Food Plants and Bare Ground are combined with a geometric mean (Fig. 2), then averaged with Mast. Percent cover of Food Plants in the field averaged 1.4% on all study areas except BC, which scored 23.0%. Corresponding SIs were 0.12 and 0.44, so Food Plants were not responsible for elevated scores. Bare Ground measures averaged 17.3% for a SI of 0.62. Mast scored the highest, with an average field value of 38.1% and resulting SIs 0.94 - 1.0 except for BC with 18.3% and SI = 0.61.

In addition to high SI scores for Mast in type DF, the equation that combined food variables raised the score. Mast was weighted double and combined with Food Plants and Bare Ground with an arithmetic mean. The mean is the least stringent function, producing scores higher than those from other functions.

Relationships between density and food in the SIs and variables of the other cover types were weak. Of 23 possible relationships, 3 were significant at $p < 0.05$ but none provided usable information.

Role of Nesting:--Nesting is a function of the presence and extent of cover types that can provide nesting habitat; the density, cover, and height of grass, and wetness of the soil; and the interspersion between those types that can and those that cannot provide nesting. When those items are combined, calculated nesting scores are weighted equally with hectares in the cover types.

Only types F, G, and PH (plus savannah on site TW) are assumed to provide nesting habitat, and they all scored > 0 so interspersion for nesting did not become a factor. Types DF, DS, and C received no scores for nesting. The most influential cover type was F. It occurred on all

9 sites, provided the largest amount of EOA (73.8 ha), and scored the highest on quality with SIs averaging > 0.80 and an LRSI averaging 0.73.

Three significant rel itionships between nesting and density were found (Table 11). They had no predictive or analytical value, however. Too little variation existed for the variable of Soil Moisture for analysis. In type F, Bare Ground showed a negative linear trend with density, and Grass Percent showed a positive linear trend. These was no discernible pattern with any other combinations.

Role of Cover:--The model assumed cover was available in types DF and DS only, and is a function of the extent of those types, any necessary interspersion calculations, and the scores for the variable cover. All scores were > 0, with an average of 0.53 in DF and 0.77 in DS. The CSI was 1.0 on 6 sites, but because it was never the lowest of the 3 LRSIs it did not contribute to the elevated scoring pattern. Density was not significantly correlated with cover in DF (-0.234) and was weakly correlated in DS (-0.553). A scatterplot showed a clear negative linear trend between density and cover in type DS.

Modification of the Model

The objective of modifying the model was to increase the strength and predictability of the relationship between HSI scores and density by reducing scatter on a scatterplot, moving the intercept towards the origin, and increasing the slope towards a value of 1.0. To accomplish this objective, a major effort was to lower the overall scoring pattern. This can be done in most models by adjusting the curves for the factors that are most influential (food or nesting, in these 9 study areas) to make optimum conditions more difficult to reach, or by changing the

Table 11. Spearman correlations of density and NSIs, SIs, and variables for nesting by cover type at the Ames Plantation, Grand Junction, Tennessee.

Cover type	Sample size	r for NSI	Variable	r for SI	r for variable
F	9	0.557	Bare ground	0.092	-0.126
			Grass percent	0.144	0.336
			Grass height	0.655[a]	0.577
G	7	0.054	Bare ground	0.614	0.205
			Grass percent	0.205	-0.205
			Grass height	0.236	0.200
PH	4	0.632	Bare ground	0.632	0.949[b]
			Grass percent	0.949[b]	0.316
			Grass height	0.632	0.632

[a] significant at < 0.10
[b] significant at < 0.05

equation to give those factors less weight.

Because of the influence of various food scores on the performance of the model, I began with food. The starting point was the minimum score function used to combine FSI, NSI, and CSI into a HSI. The original model weighted each SI equally, so I reduced the weight of food mathematically. I recalculated the HSI after multiplying the EOA by 0.25, 0.5, 0.67, and 0.75; then taking the minimum of the 3 SIs. The best result from these processes was use of the 0.5 factor, which increased the Pearson correlation with birds to 0.839, lowered the intercept to 0.212, and lowered the average HSI value to 0.32 from 0.50. It also lowered the slope to 0.344 so the birds showed an elevated pattern relative to model scores. The Spearman correlation between density and the HSI with the 0.5 factor for food EOA was 0.778 with an intercept of 1.092 and a slope of 0.782. Site MM was an outlier that depressed the correlation coefficient.

The next trial was to reduce scores by setting optimum food EOA at 90% and 100% instead of 80%, requiring food to be available over a larger part of the area. The Pearson correlation of density with HSI for the 90% and 100% curves rose slightly to 0.633 and 0.682, respectively. Slopes and intercepts showed little change, and the overall average HSI was reduced from 0.5 to 0.47 and 0.44, respectively. Scores for sites DM, HP, TE, and TW changed. Site rankings were the same for the 2 recalculated HSIs and very similar to the original HSI; Spearman correlations with density were 0.711.

The next logical point for modification was the equation that combined the SIs for Food Plants, Bare Ground, and Mast into an LRSI.

Adequate conditions of Food Plants and Bare Ground are both necessary and can partly compensate for each other, although overall suitability will be 0 if either one scores 0. Both a geometric mean and a product function meet those conditions, but a product is too rigorous a function for the low Food Plant values obtained in this study so the geometric mean was retained. An examination of the SIs from Mast showed high scores (Fig. 5), which contributed to high HSI scores. I reduced the weight of Mast from 2 to 1 to give equal weight to the units of Food Plants/Bare Ground and Mast. These units were then combined as an arithmetic mean, because 1 or other of them can provide all necessary food for the quail. I also ran equations with Mast weighted at 0.5 its value, and with several other combinations of weights and means.

When HSIs were recalculated with these equations, the Pearson correlations ranged from 0.521 to 0.689 but the approximation to a straight line was not improved. It was not possible at this point to select one equation to use in the next modifications.

A second attempt to lower Mast scores was by changing the SI curve. I raised optimum conditions from 30% to 40% and 50% and recalculated HSIs. The increase to 40% caused no change, but the increase to 50% lowered scores on sites DM and HP and raised the Pearson correlation value to 0.614.

An additional change was to set the minimum food value for the Food Plant variable at 0.05 instead of 0.10. Either score serves the same purpose of preventing that variable from scoring 0 and negating the contribution of Bare Ground, Crop Type and Management, and Mast, but those sites with very low Food Plant percentages were contributing a

larger SI to the equation than was warranted. There was a reduction in HSI score on sites DM, HP, and TE which was sufficient to increase the correlation with birds to an $r = 0.608$.

The original SI curve for Bare Ground was set to optimum conditions at 30%, and the average SI was 0.62 which also contributed to the high scores for food. Based on a Texas study (T. Doerr, pers. commun.) that found the highest number of quail associated with 55-62% bare ground, I increased the optimum level to 50-60%. That change raised the Pearson correlation to 0.592. HSI scores for sites DM, HP, and TE were lowered slightly.

These independent changes were all in the right direction but too small to be of much benefit. The next step was to combine individual food-related trials into new versions of the model. Criteria for selecting the independent changes to be used further were the strength of the Pearson correlation value, the intercept and slope of the scatterplot, mean HSI value, and simplicity and biological rationale of the food equation.

During these independent trials, I observed that the HSI score on site BC never changed from 0.52, which always made it an outlier on the scatterplots, lowered the correlations, and flattened the slope. When scatterplots for HSIs from the previously described versions of the model were run again with density and excluding site BC, more information was revealed. For example, those equations with optimum EOA set at 90% tended to plot along a straighter line than those with 80% or 100% optimum. Those with EOA at 100% tended to have lower mean HSI scores, but lower correlations as well. Use of the 0.05 minimum for

Food Plants always gave improvement. Adjusting the SI curve for optimum values of Bare Ground to 50-60% raised correlations and straightened the line of the plot.

Approximately 70 additional sets of HSI scores were generated. The "best" model at this point was from a combination of food EOA at 90%, minimum value for Food Plants and Bare Ground at 0.05, optimum levels of Mast and Bare Ground at 50-60% cover, and a food equation with Mast weighted equal to the Food Plants/Bare Ground combination:

$$\frac{(\text{Food Plants x Bare Ground})^{0.05} + \text{Mast}}{2}$$

The Pearson correlation with density was 0.748 ($n = 9$, $P < 0.02$) with an intercept of 0.259 and slope 0.450 (Fig. 7). The mean HSI score was 0.405. The Spearman correlation was 0.731 ($n = 9$, $P < 0.05$). When the scatterplot was run without site BC, the Pearson correlation rose to 0.912 ($n = 8$, $P < 0.01$) with intercept 0.196 and slope 0.814. The rank correlation without BC was 0.792 ($n = 9$, $P < 0.01$).

The 5 sites with the lowest number of birds received the lowest HSI scores (Table 12). In the rankings, only sites BC and MM were out of line. The HSI and FSI scores were effectively the same on 7 of the 9 sites. When scatterplots of FSI scores against density were examined, the Pearson correlation of 0.830 (intercept 0.271 and slope 0.637) indicated that food was still driving the model.

The scores overall remained too high and the slope of the line, with BC included, remained too flat. However, there were no other changes evident for the food component of the model. Nesting was the life requisite with the next greatest influence on HSI scores.
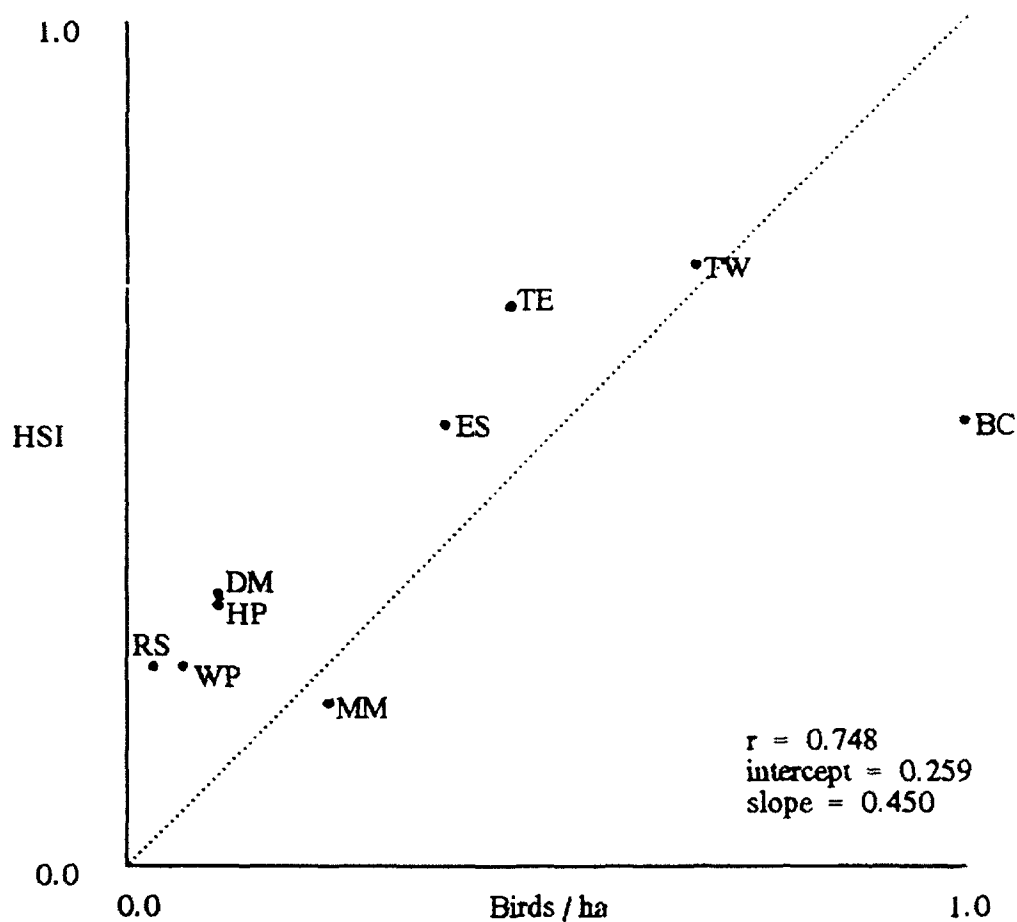
Fig. 7. Scatterplot of HSI scores and birds/hectare on each study area on the Ames Plantation, Grand Junction, Tennessee, from the revised model. Study area names were defined in Table 2.

Table 12. Comparison of ratings and rankings of density, HSI, and FSI model scores using the revised model on 9 study areas on the Ames Plantation, Grand Junction, Tennessee.

Study area	density	Ranked density	HSI scores	Ranked HSI scores	FSI scores	Ranked FSI scores
BC	1.00	1	0.52	4	0.75	2
DM	0.08	6.5	0.31	5.5	0.31	5.5
ES	0.37	4	0.52	3	0.77	1
HP	0.08	6.5	0.31	5.5	0.31	5.5
MM	0.22	5	0.18	9	0.18	9
RS	0	9	0.21	8	0.21	8
TE	0.45	3	0.65	2	0.65	4
TW	0.67	2	0.72	1	0.72	3
WP	0.04	8	0.22	7	0.24	7

Area BC was clearly limited by its nesting habitat, according to the model, as LRSIs for food and cover were 0.97 and 0.83, respectively. When a correlation analysis was run using an HSI for BC of 0.83 instead of 0.52, BC moved into a position on the scatterplot more in line with the other areas (r - 0.804, n - 9, P < 0.01, intercept 0.311, slope 0.692). Assuming adequate and accurate sampling, this meant that either the adjacent habitat was providing nesting sites which the birds would use in the spring and nesting habitat on BC was of poor quality, birds were attracted onto BC from adjacent areas for food and cover, the model was scoring nesting habitat on BC unrealistically low, or nesting was not limiting.

Adjacent lands were similar to the composition of the study area on 3 sides and separated by roads. The fourth side was unbroken forest. Lacking samples, no obvious explanation involving adjacent lands exists.

The low score for nesting on BC came from 2 sources. Estimates of Soil Moisture led to the lowest SIs on any study area, 0.86 in type F and 0.63 in type G. Through multiplication, these values modified the SIs of the other 3 nesting variables downward. Data were taken in December and Soil Moisture may be improved in the nesting season.

The second reason for low nesting scores was the relatively small area available for nesting, according to the model. Site BC had 17.6% of its hectares in cover types that were evaluated for nesting (F, G, and PH). Four of the 5 study sites on which nesting was limiting had the lowest proportion of their hectares in those cover types, 17.6 - 5.9%. The curve for Optimum Nesting required an EOA of 20% for optimum nesting conditions, but that must be present in 1-3 of the 6 cover types

present on the Ames Plantation. There is adequate information to show
that quail also will nest in types DF, DS, and C (e.g., Simpson 1976,
Minser and Dimmick 1988).

Data were not collected for nesting in those cover types, but under
the assumption that they collectively provided 10% EOA, HSI values were
recalculated for the 9 study areas. Scores increased on 5 sites
including BC and remained the same on the other 4. The correlation of
this set of HSI scores with bird numbers was higher than with the
original model (r - 0.760, n - 9, P < 0.02), but the intercept and slope
changed to 0.441 and 0.587, respectively, and mean HSI scores rose to
0.631. The same result was achieved by resetting the Optimum Nesting
curve to EOA of 10% - 1.0. This effectively made FSI - HSI, except site
BC where cover was then limiting.

Because of a paucity of information in the literature on height
requirements for grass at the nest site and the larger emphasis placed
on the presence of grass and open substrate, I modified the nesting
equation of the original model in 2 ways. The first was to delete grass
height as a variable, and the second was to reduce its weight by half by
doubling the weight on the other 2 variables. Correlation of these
versions with density were significant at P < 0.05 (0.679 and 0.746,
respectively). However, they resulted in no improvement in the features
of the scatterplot and mean HSI scores were higher were higher than the
original model.

The Texas study that found a higher percent of bare ground associated
with higher numbers of bobwhite (T. Doerr, pers. commun.) did not
differentiate between feeding and nesting habitat in that preference.

Therefore, I increased the optimum percent cover of Bare Ground to 50-60% in the nesting component of the model. Little effect was seen, except for reduced correlation and higher scores.

In that same study, the highest numbers of quail were associated with 61-69% grass cover and the lowest at 75-80%. I modified the SI curve for Grass Cover by increasing its optimum to 60-70% and scoring it at 0.05 at 100% cover. This change also produced little effect,

Because I could find no other modifications to the nesting component that were logical and that would bring the mean scores down, I made no further changes to the model. Fig. 7 portrays results from the revised version.

Spatial Relationships

The relationship between density and spatial patterns was explored with correlation analysis. The size in hectares of the study areas was not significantly correlated with density although Pearson $r = -0.401$ and the scatterplot showed a linear trend. Across all cover types, the mean size of units was negatively correlated with density at $r = -0.569$ ($n = 9$, $P > 0.10$). The number of units/hectare was positively related at $r = 0.604$ ($n = 9$, $P < 0.10$). Density was correlated with selected cover type distributions over all study sites, with an r of 0.602 with percent of the site in type F ($n = 9$, $P < 0.10$), although the points were widely scattered, and 0.574 with type C ($n = 7$, $P > 0.10$). There also was a nonsignificant and negative correlation of $r = -0.349$ with percent of type DF and $r = -0.355$ with percent of type G, and both scatterplots showed a linear trend.

Measures involving cover types DF, F, and C showed the strongest

relationship. In DF, the number of cover type units/hectare was correlated with density at $r = 0.604$, $n = 9$, $P < 0.10$. The minimum size of units in cover type DF was negatively related to density ($r = -0.616$, $n = 9$, $P < 0.10$). In cover type F, the total number of cover type units was correlated with density at $r = 0.687$ ($n = 9$, $P < 0.05$) and in type C at $r = 0.644$ ($n = 7$, $P > 0.10$). In type C there were negative relationships, i.e., $r = -0.675$ ($n = 7$, $P < 0.10$) with the mean size of unit, -0.647 with the maximum size of a unit, and -0.663 with the minimum size. The latter 2 correlations were both with $n = 7$, $P > 0.10$.

No useful relationships were observed in cover type DS or G, although density and mean size of unit in type G were correlated at $r = 0.807$ ($n = 7$, $P < 0.02$). Sample size in cover type PH was too small and the relationships too ill-defined to get significant results.

The correlation between Fried's Index and density produced an $r = 0.590$ ($n = 9$, $P < 0.10$. Site TW had the highest index value. The Index for sites RS (no birds) and BC (highest number of birds) were intermediate. Three of the sites with fewest birds had the lowest Index (DM, HP, and WP). There were no relationships evident between density and the perimeter of the site or the ratio of perimeter to hectare. Index values were between 0.1211 and 0.1400.

DISCUSSION

Rejection of the Null Hypothesis

A significant and positive relationship was found between bobwhite population density and HSI model scores. Therefore, the null hypothesis of no relationship was rejected. Jones and Matloff (1986:1156) argued against hypothesis testing, saying that the most relevant information is "the magnitude of the differences between treatment effects, or the goodness of approximation of a scientific proposed model (theory)". They go on to say that results of hypothesis testing are inadequate and can be misleading. Inadequate and misleading results can come from any analysis, and the real message is that reliance on statistical test results without interpreting their meaning to the object of study is poor science.

The meaning of these test results lies both in the strength and direction of the relationship seen. Both characteristics are important to users of the model. The size of the correlation coefficient indicates how much of the variability of the system is explained, in this case, how well the model can reduce bobwhite habitat needs to a single number. The slope shows the extent to which output is linearly consistent, so that comparisons can be made among any points on the 0.0 to 1.0 scale. The intercept tells how similar the 2 axes are in relation to each other. The correlation coefficient and slope are the 2 most important features for a HSI model. If the intercepts differ, 1 or the other scale can be manually or mentally adjusted.

With the revised version of the model, a correlation coefficient of 0.748 explains 56% of the variability in the relationship between

density and HSI scores; 44% of the variability remains unexplained. This is an improvement over the original model which had an r^2 of 34%, but less improvement than hoped. With another population of field sites in western Tennessee, a person using the revised model would have just over a 50% chance of rating the sites correctly. The likelihood of ranking the sites correctly is higher, because model scores at 7 out of 9 sites or 78% were in agreement with density of bobwhite.

Has this model been validated? Hall and Day (1977) equated validation with hypothesis testing in that neither a hypothesis nor a model can be proven to be true or correct. Validation has been associated with the concept of adequacy (Hall and Day 1977), which leads to the opinion by Morrison et al. (1987:252) that a "model is adequate if it supplies the level of resolution required by the user".

Performance of the Model

There is a variety of opinion in the literature on how to determine adequacy of a model, or how to judge and interpret model performance. Perhaps the most generous opinion is from Gotfryd and Hansell (1985:231) who wrote "...ecological models may be built and tested without the benefit of knowing the truth or even the proximity of the data to the truth. It is often adequate if the data are consistent and reflect differences between situations." McDonnell et al. (1984) provided an example of this scale with a model test on the impacts of lakeshore development on small mammals. They were satisfied with the model's performance for planning purposes, and satisfied that they had increased their understanding of the limits of the model.

At the other end of the scale lie defined standards such as Green's (1979) definition of perfect models as having generality, realism, and precision. Cale et al. (1983) measured model utility or applicability by the concepts of adequacy and reliability, using theoretical equations to define boundaries around model functioning. They gave criteria for desirable models and a list of principles for increasing model desirability.

Is this HSI model adequate? To answer that question, the uses and users must be defined. Uses of HSI models vary from a quick planning study to determining a management prescription that will cost money and time to an analysis that will withstand legal attention. As it exists now, I would recommend use of the entire bobwhite HSI model for a planning study, with data collected for the variables as estimates. I would recommend its food and spatial components for use in writing a management prescription, e.g., determining limiting factors and locations for management practices. I would probably not recommend the model for any purpose requiring additional rigor.

The draft model was written to be applicable over the entire range of the bobwhite and in theory would be tested in all parts of this range prior to applications. In practice, if the model were published, it would be applied by users in any state with bobwhites. I would recommend users outside western Tennessee test the model with the best census data available and modify the model appropriately prior to use. If census data are not available, an expert in bobwhite habitat needs should be asked to provide surrogate census data in the form of expert opinion ratings or rankings (O'Neil 1989). If expert opinion scores

cannot be obtained, a review and suggestions for tailoring the model to its expected application should be solicited from an expert. At a minimum, users should modify the model to fit local conditions as they know them.

Comments on the Performance of the Model

The determinants of the outcome of a HSI model test are the model subject, content, and structure; data on habitat features; suitability of and data on a standard of comparison; and study design and analysis. These items form the basis for observations on conduct of this study.

Model:--The model begins with assumptions about the importance of habitat with adequate amounts of food, cover, and nesting sites. Klimstra and Roseberry (1975) and Dimmick (1974) both attributed a large proportion of the variability in quail populations to nesting success. The model scores at the Ames plantation could lead to the conclusion that only the food components of the model are needed. However, to maintain larger applicability of the model, the assumption of the importance of nesting habitat must be maintained.

From this model test, it was not evident that any of the 9 base variables or their SIs contributed to the relationship between density and HSI scores. Relationships were seen when the 3 spatial variables were factored in. That raises the question of whether spatial considerations alone (e.g., distance between cover types) might be sufficient to derive a HSI score. On the Ames Plantation where cover type diversity and interspersion are generally high, that may be true. On sites where diversity and interspersion are lower, the non-spatial variables may show equal or greater importance.

Models with simpler structure are easier to understand and modify. The HSI models for species that use more than 1 cover type are inherently more complex than models for single cover type users and often contain more variables than is desirable. That is true with this model, so that predicting how the model would react to a modification was difficult. For example, I saw very similar results with many different trials, and often very little change when I expected more. In addition, although the variables themselves were not complicated, the model structure was deceptively complex. An example of this complexity is the use of a geometric mean in the food component. The size of the difference between the 2 SIs that enter the equation determines how severely reduced the product of the calculation will be. When the difference between SIs is greater, the final result is relatively lower than when the difference is smaller.

Habitat features:--Data on habitat features should have been collected in continuous fashion regardless of the form of the original SI curve (e.g., Cover). Without continuous data, I could not apply the same type of analysis to that variable as to the others. The sensitivity of the model to the low values for Soil Moisture estimates in the nesting component indicated that Soil Moisture should have been recorded at greater resolution, possibly in 5 categories instead of 3. Although the sensitivity of that variable might warrant continuous data, that level of effort would be unreasonable to expect of most model users.

Potential additional variables also should have been measured, e.g., percent of total vegetative cover in nesting cover types. Nesting

variables should have been measured in cover types specified as non-nesting by the model (DF, DS, C). In cover type C, only no-till fields would have been included (Minser and Dimmick 1988).

Based on the appearance of the sites and results of bird census, this study had the necessary range of apparent habitat quality at a large scale. At a smaller scale, some variables showed insufficient differences across sites to be of much utility in separating sites with the model.

Some habitat variables were interrelated, and those with the strongest relationship could have been removed from further consideration. However, Bare Ground, the variable with the strongest associations, was negatively correlated with others. That indicated an important relationship that should be maintained.

Standard of comparison.--When the standard of comparison used in a model test is the number of birds counted, it is assumed that the census methods accurately portray bird abundance and that the abundance of birds reflects habitat quality. If either assumption is not true, the model test loses validity.

Our ability to accurately determine population levels of wildlife species is variable. However, for bobwhite in western Tennessee, the accuracy of the walk census has been identified in comparison to the Lincoln Index (Dimmick et al. 1982). Application of the technique for this study was consistent with documented practice.

Whether the resulting abundance of birds was positively and linearly related to habitat quality is less certain. Errington (1934) wrote about overflow of bobwhite from areas with populations higher than

carrying capacity into areas of poorer habitat quality; a census and habitat study in those circumstances could find a mismatch of birds and habitat quality. A study by Darrow et al. (1981) included bobwhite "to determine whether amount of wildlife use of the study sites was reflected in habitat scores derived for those sites". Although the habitat appeared adequate, recent severe winters were thought to have depressed bobwhite populations and no birds were found.

Even if census results are ultimately related to habitat quality, there are many proximate factors that can interfere with an anticipated relationship. Overriding factors such as weather can occur; McRae et al. (1979) linked drought conditions with lower legume production which could lower overwinter survival of quail. Only some percentage of the variation in populations can be explained by habitat factors. Most definitions of carrying capacity, for example, also include interspecific and intraspecific relationships, factors of climate and weather, disease, etc.

Study design:--Two common points of discussion for study design and analysis in habitat studies are the need for large sample sizes and the adequacy of 1 year of data as opposed to data collected over time. A sample size of 9 is less desirable from a statistical perspective than a higher number, and I would have preferred a sample of about 15. Nine is unfortunately not atypical for HSI model tests (Table 1). Biologically, the range of variation exhibited by the 9 sites on the Ames Plantation alleviated the small sample size to some degree.

Use of data from 1 year elicits comments either that relationships seen are coincidental, or that relationships were not seen because the

year was "abnormal" in some way. For a species whose numbers generally reflect habitat conditions so closely, attempting to relate habitat data to same-year census data is valid. It would, of course, be more desirable to link the same habitat features with census data over several years.

A third point is the type of analysis. With a small sample size, some of the more sophisticated techniques are not appropriate (Green 1977). In addition, interpreting their output becomes more difficult; Meents et al. (1983) encountered difficulty in interpreting the biological meaning of multiple regression steps past the first 2. Correlation analysis is relatively simplistic, but has high utility for this kind of test.

Benefits of correlation analysis and associated scatterplots include depiction of the relationship of all data points, i.e., how each site fits with the others; detection of pattern, therefore clues as to why there is or is not a statistical relationship; and existence of outliers, to be used to catch errors and as an exploratory aid (Light and Pillemer 1984). Disadvantages include no determination of cause and effect; the presence of intercorrelations, leading to bias and confusion; possibility of spurious self-correlations (Kenney 1982); and the fact that items may covary but for no intuitive reason, i.e., significant but not biologically meaningful relationships.

Effect Size

If the magnitude of difference (between treatment effects, Jones and Matloff 1986) is the most useful piece of information from a test, then

how large does that difference have to be before it is useful?
Significant but relatively low correlation values are often reported and
then used as the basis for additional analysis. If r = 0.6, 36% of the
variability in that relationship is explained. However, 64% is not
explained. The amount of explanation that can be _expected_ from a test
should be considered before deciding whether the results are sufficient.

By definition, models do not include all parameters that might affect
the system being modeled (Hall and Day 1977). In HSI models, many
relevant environmental variables, factors of known importance to an
animal's well-being and productivity, are excluded (Schamberger and
O'Neil 1986). Therefore, expectations for perfect correlation between
model output and standard of comparison are unreasonable.

Power of a test (probability that a test will result in rejection of
the null hypothesis when it is false) is a function of the alpha level,
sample size, and Effect Size (Rotenberry and Wiens 1985). Effect Size
could be the magnitude of the difference between treatment effects
(Jones and Matloff 1986), or "the magnitude of the departure from the
null hypothesis" (Rotenberry and Wiens 1985:164). In the context of
this study, I interpreted Effect Size as the percent of the animal
response (bobwhite density) that could be explained by the HSI model.

Marcot (1986:203) wrote that typically only 50% of the "variation in
species' abundance is accounted for by habitat variables alone".
Rotenberry and Wiens (1985) found explanatory value in a correlation of
determination of 25% in discussing competition among western passerines.
Suggestions for study design to determine "maximum attainable R^2" were
presented by Marzluff (1986:167).

If Effect Size is 50%, then relevant and useful correlation levels are r - 0.7 or higher. The final correlation coefficient from this study met that criterion.

Additional Work

The primary objective of this study was to produce a model whose HSI score matched an indication of population density on each of the 9 study areas on Ames Plantation in 1983. To the degree I was successful, the result is a model "designed to fit the data" (Cale et al. 1983:179), but the total information content and utility of the model is unknown. To expand its utility will require additional data sets and testing.

Additional testing of this model and habitat relationships of the bobwhite should occur in locations distributed over its range. Systems and conditions that require special attention include those with harsher winter, drier climate, and fewer mast items. Applications are needed in different seasons, e.g., nesting conditions should be examined in late winter or early spring. In all tests, current and potential variables including those for spatial relationships among cover types should be measured.

SUMMARY AND CONCLUSIONS

A HSI model for the northern bobwhite was tested at 9 study areas on the Ames Plantation near Grand Junction, Tennessee. The model included variables to portray the bobwhite's needs for food, cover, and nesting habitat; and the distribution of areas that provide those needs. The variables are combined through graphs and mathematics into a number between 0 and 1, with 1 representing optimum habitat conditions.

The 9 study areas were divided into homogenous cover types of deciduous forest, deciduous shrubs, forbland, grassland, pasture/hayland, and cropland. Data on the variables were collected in September 1983 and a HSI score calculated for each study area. Selected spatial measurements were derived to provide potential alternate model variables.

Census data were collected in December 1983 by a walk census. Alternate expressions of bird density were examined, for example, total number of birds and number of coveys. The number of birds/hectare indexed to 1.0 was selected as the standard of comparison to determine the amount of agreement between model scores and census results.

Censuses produced quail numbers between 0 and 3.28 birds/ha with a mean of 1.0/ha. Initial model scores were between 0.19 and 1.0 with a mean of 0.5. Food was the limiting factor on 3 areas and nesting cover was limiting on 5 areas. One site scored optimum for all conditions.

Density was correlated with HSI scores (Pearson r = 0.582, n = 9, P < 0.10, Spearman r = 0.711, P < 0.05). A scatterplot of the Pearson analysis showed 4 sites below the regression line and 4 above. The model scores were higher than density on 7 of the 9 study areas.

Assuming census data accurately reflected habitat quality, I searched
for the factors with the strongest influence on the model to determine
the reason for the elevated scores. Several internal components of the
model pertaining to food were highly correlated with density.
Components pertaining to cover, nesting, and spatial considerations were
either not significantly correlated with density or their relationship
had no predictive value.

Again assuming the census data accurately reflected habitat quality,
the model was modified to make the scores on each study area more
closely approximate census results. Modifications included adjustments
in equations and weights to lower the relative weight of food compared
to the other life requisites. When the best fit was reached, the
Pearson r rose to 0.748, $n = 9$, $P < 0.02$, and the Spearman $r = 0.731$, P
< 0.05. On the study area with the most birds, the score was 0.52 with
nesting limiting according to the model. An additional set of
modifications attempted to bring up the score for that study area by
adjusting nesting factors. However, no modifications were effective and
logical, so the revised model based on changes in food components
remained in place. No relationships between spatial measurements and
density were sufficiently strong to provide variables for the model.

The following points are the primary conclusions:

1. Quail populations on the 9 study areas represented an adequate range
of conditions from poor to high quality. Initial model scores also
occurred over a range of possible values. Internal components of the
model were mixed in their range of occurrence.

2. According to the model, factors related to food were limiting on 3

study areas and factors related to nesting were limiting on 5 other areas. Cover was never limiting. Interspersion of cover types was very high.

3. Factors related to food were the most influential in relationships between model output and density. Food variables were responsible for the elevated scoring pattern, with the deciduous forest the most influential cover type.

4. The initial correlation between HSI scores and density was significant but with less predictive value than desired. Accuracy was low compared to census results, with the model scoring sites higher than density.

5. Acceptable results (agreement between model scores and census results) were reached with the revised model. Model performance in ranking sites was better than in rating sites. The model has utility in planning and management in environments of west Tennessee. Application in other locations and for more rigorous purposes would require additional testing and adjustment of the model.

6. Spatial measures were less strongly related to density than expected, based on previous studies and the natural history of the bobwhite. Because interspersion of cover types was so high, spatial factors were not limiting at the Ames plantation. Measures that were significantly correlated with density were positively related to diversity of cover types.

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13. ABSTRACT (Maximum 200 words)

    A draft Habitat Suitability Index (HSI) model for the northern bobwhite (*Colinus virginianus*) was tested on nine study areas at the Ames Plantation, Grand Junction, Tennessee. The standard of comparison for the test was number of birds per hectare determined from walk-census data obtained in December 1983. Density ranged from 0 to 3.28 birds/ha, and initial HSI scores ranged from 0.19 to 1.0. Density was significantly correlated with HSI scores, but model scores were higher than density on seven of the nine study areas. Factors in the model related to food were responsible for the elevated scores. Assuming census data accurately reflected habitat quality, the model was modified to make the scores more closely approximate density estimates. The resulting model scores correlated with density at Pearson $r = 0.748$ ($n = 9$, $P < 0.02$). Performance of the model is adequate for planning and management purposes in west Tennessee. Application in other locations and for more rigorous purposes would require additional testing and adjustment of the model.

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